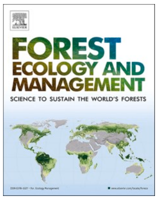
Forest Ecology and Management 512 (2022) 120129

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Tamm reviews

# Mechanisms of forest resilience

Donald A Falk[a,e,*], Philip J van Mantgem[b], Jon E Keeley[c], Rachel M Gregg[d], Christopher H Guiterman[e,1], Alan J Tepley[f], Derek JN Young[g], Laura A Marshall[h]

[a] *School of Natural Resources and the Environment, University of Arizona, Tucson, AZ, USA*
[b] *U.S. Geological Survey, Western Ecological Research Center, Redwood Field Station, Arcata, CA, USA*
[c] *U.S. Geological Survey, Western Ecological Research Center, Sequoia and Kings Canyon Field Station, Three Rivers, CA, USA*
[d] *Environmental Science Associates, Seattle, WA, USA*
[e] *Laboratory of Tree-Ring Research, University of Arizona, Tucson, AZ, USA*
[f] *Northern Forestry Centre, Canadian Forest Service, Edmonton, Alberta, Canada*
[g] *Department of Plant Sciences, University of California Davis, Davis, CA, USA*
[h] *Forest & Rangeland Stewardship Department, Colorado State University, Fort Collins, CO, USA*

## ABSTRACT

Ecosystems are dynamic systems with complex responses to environmental variation. In response to pervasive stressors of changing climate and disturbance regimes, many ecosystems are realigning rapidly across spatial scales, in many cases moving outside of their observed historical range of variation into alternative ecological states. In some cases, these new states are transitory and represent successional stages that may ultimately revert to the pre-disturbance condition; in other cases, alternative states are persistent and potentially self-reinforcing, especially under conditions of altered climate, disturbance regimes, and influences of non-native species. These reorganized states may appear novel, but reorganization is a characteristic ecosystem response to environmental variation that has been expressed and documented throughout the paleoecological record. Resilience, the ability of an ecosystem to recover or adapt following disturbance, is an emergent property that results from the expression of multiple mechanisms operating across levels of organism, population, and community. We outline a unifying framework of ecological resilience based on ecological mechanisms that lead to outcomes of persistence, recovery, and reorganization. Persistence is the ability of individuals to tolerate exposure to environmental stress, disturbance, or competitive interactions. As a direct expression of life history evolution and adaptation to environmental variation and stress, persistence is manifested most directly in survivorship and continued growth and reproduction of established individuals. When persistence has been overcome (e.g., following mortality from stress, disturbance, or both), populations must recover by reproduction. Recovery requires the establishment of new individuals from seed or other propagules following dispersal from the parent plant. When recovery fails to re-establish the pre-disturbance community, the ecosystem will assemble into a new state. Reorganization occurs along a gradient of magnitude, from changes in the relative dominance of species present in a community, to individual species replacements within an essentially intact community, to complete species turnover and shift to dominance by plants of different functional types, e.g. transition from forest to shrub or grass dominance. When this latter outcome is persistent and involves reinforcing mechanisms, the resulting state represents a vegetation type conversion (VTC), which in this framework represents an end member of reorganization processes. We explore reorganization in greater detail as this phase is increasingly observed but the least understood of the resilience responses. This resilience framework provides a direct and actionable basis for ecosystem management in a rapidly changing world, by targeting specific components of ecological response and managing for sustainable change.

## 1. Introduction

Ecological communities, and the species that comprise them, are always in a state of flux in response to environmental variation. Nonetheless, the pace and magnitude of observed ecosystem change in recent decades appears to exceed recorded rates of change over recent centuries and even millennia (Barnosky et al. 2011, Scheffers et al. 2016, IPCC 2018, Nolan et al. 2018, Turner et al. 2020). Observed and projected changes for forest ecosystems include accelerated mortality among long-lived organisms such as trees (Bennett et al. 2015, McDowell et al. 2016), tree recruitment and forest regeneration failure in established populations (Stevens-Rumann et al. 2018, Davis et al. 2019), and rapid changes in species distributions (Chen et al. 2011, Burrows et al. 2014, Talluto et al. 2017). Because of the broad spatial scale of climatic impacts, and the increasing cumulative extent of ecosystem disturbances and non-native species invasions (including pests and pathogens), projected changes in ecological communities represent a massive upheaval and reorganization of ecological communities over broad regions of the globe (McDowell et al. 2020).

One consequence of increasing acute and chronic stress from these

---

[*] Corresponding author at: School of Natural Resources and the Environment, University of Arizona, Tucson, AZ 85721, USA.
*E-mail address:* dafalk@arizona.edu (D.A. Falk).
[1] Cooperative Institute for Research in Environmental Sciences, University of Colorado, Boulder, CO, USA.

https://doi.org/10.1016/j.foreco.2022.120129
Received 11 November 2021; Received in revised form 18 February 2022; Accepted 22 February 2022
Available online 24 March 2022
0378-1127/© 2022 Elsevier B.V. All rights reserved.

profound environmental changes is that forest ecosystems are being pushed outside of their recent observed ranges of variation into alternative ecological states, such as conversion of forest or shrub-steppe to self-reinforcing flammable grasslands (Balch et al. 2013, Syphard et al. 2019, Batllori et al. 2020, O'Connor et al. 2020, Landesmann et al. 2021). In some instances, these new states are transitory and represent successional stages that may ultimately lead back toward the pre-disturbance condition; elsewhere, alternative states are persistent and potentially self-reinforcing, especially under prevailing conditions of altered climate, disturbance regimes, and presence of non-native species.

Community-level change in forest vegetation is driven largely by individual species responses and interspecific interactions across spatial scales (Gleason 1926). In some cases, communities change as certain species are excluded by disturbance, competitive interactions, loss of key symbionts or mutualists, or persistent changes in key soil or hydrological resources. Community-level change can also occur when species reach a limit of tolerance in key niche parameters driven by shifting climatic zones (Notaro et al. 2012, Shirk et al. 2018), ultimately altering demographic balances of local extirpation and colonization (Comte et al. 2014, Talluto et al. 2017). This filtering process of change and adaptation, abundantly evident in the paleoecological record, includes adaptation to variable and novel environments and novel disturbances (Jackson et al. 2009, Crausbay et al. 2017). In the current era of rapid climatic change, the pace of change over the landscape (climate velocity) may exceed the capacity of species to adapt through either geographic movement or evolutionary change (Davis et al. 2005, Colwell and Rangel 2009, Loarie et al. 2009, Brito-Morales et al. 2018). The result is an increasing occurrence of potentially irreversible change and reorganizing of ecological communities.

### 1.1. *A framework for ecological resilience*

Ecological resilience can be decomposed into three distinct components operating at different levels of biological organization: persistence, recovery, and reorganization, each with a distinct set of underlying mechanisms (Millar et al. 2007, Falk 2017, Falk et al. 2019). *Persistence* is the ability of individuals to tolerate exposure to environmental stress, disturbance, or competitive interactions. Persistence is the most direct expression of life history evolution and adaptation to environmental variation and stress, and is manifested in survivorship and continued growth and reproduction of established individuals. Persistence also provides the highest degree of continuity with the pre-disturbance community, maintaining a wide range of ecological legacies (Higgs et al. 2014, Johnstone et al. 2016).

When persistence has been overcome (e.g., following widespread mortality events), populations must *recover* by reproduction. Recovery requires the establishment of new individuals from seed or other propagules following dispersal from the parent plant. Population recovery is particularly sensitive to the environmental conditions required for germination, establishment, and growth of young individuals, as well as inter- and intra-specific interactions. Both persistence and recovery tend to result in a community with a high degree of similarity to the pre-disturbance state.

When recovery fails to re-establish the pre-disturbance community, the ecosystem will *reorganize* into a new state (Beisner et al. 2003). Community reorganization occurs along a gradient of magnitude, from changes in the relative dominance of species already present in a community, to individual species replacements within an essentially intact community, to complete species turnover and a shift to dominance by plants of different functional types, e.g. transition from forest to shrub or grass dominance (Fletcher et al. 2014, Guiterman et al. 2018, Miller et al. 2019). These reorganized states can be persistent or transient depending on ongoing disturbance, climatic suitability, and competitive relationships. When reorganization is persistent and involves reinforcing mechanisms, the resulting state is termed a *vegetation type conversion* (VTC), which in this framework represents an end member of reorganization processes (Kitzberger et al. 2016, Syphard et al. 2019, O'Connor et al. 2020).

Resilience, the ability of a vegetation community to recover or adapt following disturbance, is thus an emergent outcome that results from the expression of multiple mechanisms operating at levels of organism, population, and community interaction (Fig. 1). Each primary element of resilience (persistence, recovery, reorganization) reflects a set of mechanistic processes that must be understood in order to interpret and predict ecosystem responses.

In this paper, we summarize existing observations of forest vegetation persistence, recovery, and reorganization across levels of biological organization, and explore the primary mechanisms that regulate these processes (Table 1). Our objective is to provide a detailed, mechanistic framework for the science of ecological resilience in forests and its application to ecosystem management (Millar et al. 2007, Falk 2017, Coop et al. 2020, Stevens et al. 2021, Guiterman et al. in preparation). We provide examples of these processes in the literature, focusing on forests of western North America but with additional cases from other regions.

## 2. Mechanisms of persistence

Persistence is the ability of individuals to survive disturbance, be it stressful droughts or biophysical destruction such as fire. This section deals with mechanisms of how individuals in a population survive these disturbances. We illustrate the mechanistic basis of persistence using two widespread stressors: wildfire and drought.

### 2.1. *Individual tree persistence: Fire*

Fire is one of the more ubiquitous forms of disturbance in forest ecosystems, and a significant influence on species evolution (Gagnon et al. 2010, Pausas et al. 2017). However, even plant communities dominated by fire-adapted species encounter perturbations that are outside the fire regime to which they are adapted, which can result in mortality and loss of reproductive capacity, coupled with community reorganization (Keeley and Pausas 2019). During wildfire, heat is transferred to all parts of the plant by various energy transfer mechanisms, requiring specific anatomical and physiological adaptations (Michaletz and Johnson 2007).

The evolutionary response to fire generally follows one of two pathways: through niche selection for environments that avoid fire, or by developing morphological characteristics that allow the plant to survive fire (Rowe 1983, Clarke et al. 2015). In relatively productive environments, especially those with strong seasonality that provide a dry period sufficient to convert biomass to flammable fuel, fire is a predictable feature of the environment, and traits that confer resistance to fire are selected. These traits include thick insulating bark, self-pruning of dead branches, or resprouting from protected buds (Keeley and Zedler 1998, Pausas 2015).

The temporal scale of predictability of fire varies with climate and biome. For example, Mediterranean climate ecosystems experience conditions that potentially allow fire every summer and fall; dry temperate forests generally carry fire during dry spring or early summer weather (Arizpe 2016), whereas mesic and boreal forests are fire-prone primarily during multi-annual to decadal scale climate events (Gedalof et al. 2005). These regimes represent very different evolutionary environments: trees in the former areas have higher levels of persistence following fire (at least when fire burns within its historical range of variation in fire behavior), whereas in the latter areas, individuals are generally killed by fire, and populations rely primarily on post-mortality reproduction.

#### 2.1.1. *Surface fire regimes*

Western North American mixed conifer forests are moderately

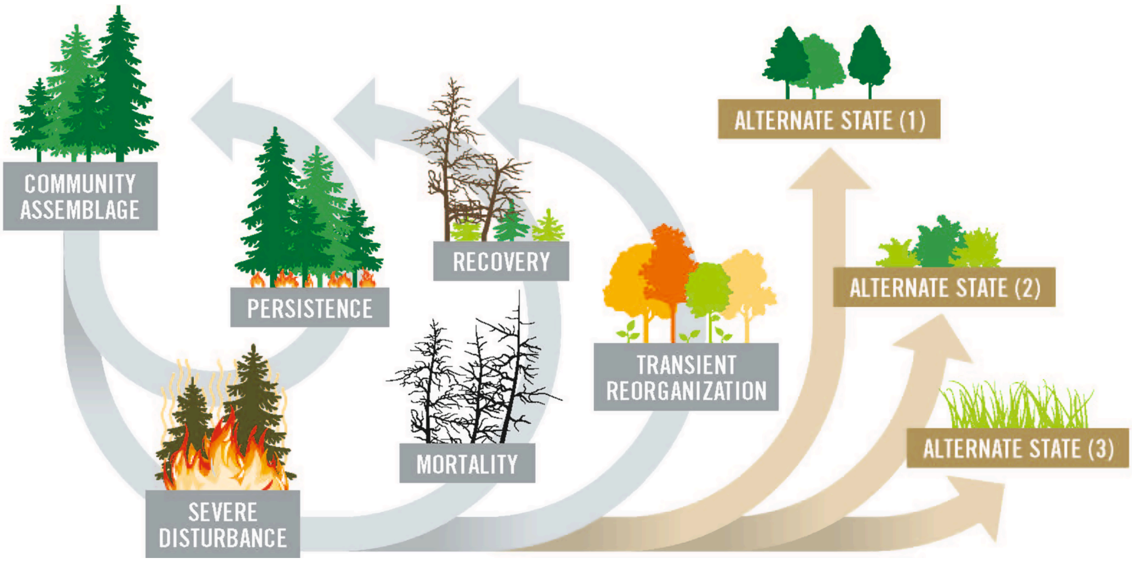


**Fig. 1.** A unified framework for ecological resilience. Individuals persist through levels of disturbance to which they are adapted, but mortality occurs when these thresholds are exceeded. Recovery is a population-level process that requires establishment of new individuals from seed or other propagules following dispersal from a parent plant, eventually creating a new replacement population. When recovery fails or is impaired, community-level reorganization occurs, involving different species or functional groups. Reorganization can be transient, leading to eventual re-establishment of the pre-disturbance community, or leading to alternative metastable states that are reinforced by disturbance and/or climate.

productive ecosystems where growth rates are sufficient for the canopy to outgrow surface fuels. This creates a spatial gap between surface and canopy fuels, increasing the likelihood of tree survival. This persistence strategy is globally widespread in seasonal environments where natural lightning ignitions are predictable during the dry season (Williams et al. 1999, Hoffmann et al. 2003). Discontinuity between surface and canopy fuels is a common feature of both coniferous forests and oak woodlands in the northern hemisphere, as well as in tropical savanna trees (Hoffmann et al. 2003) and the drivers of persistence are tied to multiple morphological and ecological parameters (Hood et al. 2018, Furniss et al. 2019, van Mantgem et al. 2020b).

Frequent fire regimes select for traits that enhance survival. The abscission of lower branches is a critically important adaptation that increases the spatial gap between surface fuels and the tree canopy, placing live branches above characteristic flame length and plume of combustion gases, as well as protecting the lower stem cambium (Fig. 2.a) (Keeley and Zedler 1998, Schwilk and Ackerly 2001). This trait is well developed in many trees adapted to frequent surface fire regimes, but is largely absent in those species found in high intensity crown fire regimes (Keeley 2012). The exposure of aboveground plant parts (stems, branches, foliage) to aboveground flaming combustion may be relatively short (minutes), but residence time of belowground smoldering combustion can extend to hours or days, exposing fine roots to extensive mortality (Michaletz and Johnson 2007).

Since the lower stems of trees cannot escape direct exposure to surface fires, a critical potential stress is heat penetration, which can be lethal to the underlying cambium cells at temperatures above 60 °C (Bauer et al. 2010). Many fire-adapted pines have developed heat-resistant bark that protects the critical growth layers of the cambium (Fig. 2.b). The insulative capacity of bark is affected most strongly by bark thickness, although other characteristics such as surface structure and density play a role (Michaletz and Johnson 2007, Wei et al. 2020). Thick bark is more common in fire-prone ecosystems (Rosell et al. 2017) and is associated with higher survival (Ryan and Reinhardt 1988), although this depends largely on the fire regime. The importance of bark thickness increases with age, as survivorship of young trees is favored more by height growth (Kidd and Varner 2019). For example, arborescent oaks subject to frequent surface fires have relatively thick bark (Pellegrini et al. 2017), distinctly unlike the thin bark of scrub oaks in infrequent-fire regimes (Zedler 1995); this is also true of pines (Keeley and Zedler 1998) and a variety of other tree species (Pausas 2015).

Bark thickness evolves in response to other environmental drivers, such as protection from heat, cold, and insects; however, in pines it is associated strongly with species in surface fire regimes and is not found in species adapted to arid or alpine conditions (Keeley and Zedler 1998). Across a wide spectrum of tree clades, thick bark is not markedly associated with climate (Rosell 2016, Schubert et al. 2016, Rosell et al. 2017). Complicating our understanding of the role of bark in affecting persistence is the marked changes in bark characteristics with growth form and tree size. Allometric relationships of tree size and bark thickness produce divergent patterns in different climates, further complicating interpretations (Jackson et al. 1999, Schwilk et al. 2013). Despite its importance to persisting through fire disturbances, bark characteristics are just one set of traits that characterize species in surface fire regimes, along with physiological properties such as rapid wound response (Smith et al. 2016, Varner et al. 2016).

Although there are clear species-specific differences in capacity to persist in the face of recurrent surface fires, there is finer scale variation both spatially and temporally. Within a forest there are microsites with anomalous fuel accumulation that can be lethal to even the most fire-resistant species, especially as a result of recent forest management practices (Jeronimo et al. 2020). Conversely, topography and spatial variation in fuels can create refugia that allow the persistence even of fire-sensitive species. Persistence of individual trees following fire is also affected by environmental conditions (such as drought), biotic interactions, and topographic patterns (Schwilk and Keeley 2006, van Mantgem et al. 2018, Furniss et al.2022). Thus, while persistence traits vary with different fire regimes, those regimes are not static and vary both spatially and temporally.

This effect is further complicated by changes in climate, which in some regions have led to longer fire seasons and increasingly severe fire weather, resulting in higher fire intensities, larger areas burned, and larger high-severity patch sizes (Kitzberger et al. 2017, Williams et al. 2019). However, the complexity of wildland fire across spatial scales makes it difficult to separate the relative importance of a more than century of fire exclusion from climate change (Collins et al. 2019). Nor is it clear how climate change will affect tree persistence through changing fire regimes; some research predicts that increasing temperatures will

**Table 1**
Main components of resilience operating at varying levels of biological organization, primary processes, and key mechanisms of ecological resilience. Literature references provided in main text.

| Outcome (level of organization) | Process | Mechanisms |
|---|---|---|
| **Persistence (individual)** | Anatomical and physiological resistance to heat exposure from fire | Thick bark insulates cambium cells from heat flux, preventing necrosis; abscission of lower branches prevents spreading combustion into canopy |
| | Wound responses to fire damage | Wound compartmentalization prevents infection of lesions and damaged tissue; growth closure repairs cambial continuity |
| | Vegetative regrowth capabilities | Basal and epicormic resprouting capacity; non-structural carbohydrate storage and mobilization |
| | Drought survival, maintenance of essential functions | Plant hydraulic traits prevent xylem cavitation and embolisms; isohydric and anisohydric stomatal regulation |
| **Recovery (population)** | Post-fire propagules from *in situ* sources | Recruitment from soil and canopy seed banks, advance regeneration. Heat- and smoke-cued germination. |
| | Post-fire dispersing propagules | Wind-, gravity-, and animal-mediated seed dispersal from nearby unburned areas or refugia; continued seed rain |
| | Germination, seedling survivorship, and growth | Species-specific seed and seedling climate envelopes and microhabitat; post-disturbance weather; rooting access to mineral soil |
| | Interspecific and community interactions | Interspecific interactions may facilitate (e.g. amelioration of microclimate) or inhibit (resource competition) seedling and sapling survivorship and growth; interactions may be temporally variable |
| **Reorganization (community)** | Gradual reorganization in response to changes in mean conditions | Shifting species geographic ranges during periods of rapid climate change |
| | Reorganization in response to the loss of formerly frequent disturbance | Increased relative abundance of mesophytic species in deciduous forests, increased forest density in dry conifer forests following fire exclusion; conversion of grasslands and savannahs to closed-canopy woodlands |
| | Rapid reorganization in response to novel disturbance | Forest loss from extensive tree mortality, followed by recruitment failure |
| | Trigger events | Mortality over large contiguous areas from uncharacteristically high-severity wildfire in ecosystems adapted to frequent low-severity fire regimes. Widespread forest die-off from extended drought and episodic heat waves and associated insect outbreaks.<br>Recruitment failure in fire-tolerant and serotinous forests and chaparral due to uncharacteristically short fire return intervals |
| | Open resource space following extensive mortality | Shuffling of species relative dominance based on plant functional capacity (resprouting, obligate seed recruitment) and disturbance-cued germination |
| | Recolonization failure | Dispersal limitations in large high-severity patches beyond seed dispersal distance; germination failure of dispersed seed in severely altered post-fire environments (soil, microclimate, microbial symbionts); short fire return intervals |
| | Landscape species pool | Pre-disturbance species depend on dispersal from limited remaining refugia; rapid dispersing and early successional species able to establish in post-fire environment |
| | Community reassembly, hysteresis | Interactions among species colonizing the post-disturbance environment through biotic and abiotic filters, leading to novel community assemblages and potential alternative metastable state |
| | Reinforcing feedbacks | Invasion of non-native annual grasses into woody communities when fire regimes are perturbed, leading to conversion to persistent novel grass-fire cycle. Soil and hydrological alteration prevents recolonization<br>Climate trends (temperature, precipitation, VPD) and episodes (e.g. heat waves) prevent recruitment of prior dominant species and favor better adapted species, creating novel community assemblages |

produce more intense fires with greater tree mortality (Halofsky et al. 2020), whereas other models forecast changes in vegetation structure that will decrease fuel mass and availability and thus decrease fire intensity (Pausas and Paula 2012, Batllori et al. 2013, Hurteau et al. 2019).

### 2.1.2. *Crown fire adaptations*

Crown fires by definition involve exposure of apical meristems and foliage to radiant and convective heat and potential tissue necrosis (Michaletz and Johnson 2007). Resprouting is a mechanism that allows individual regrowth from buds following major biomass loss (Clarke et al. 2015). Many woody angiosperm genera (e.g., *Eucalyptus* L'Her., *Quercus* L., *Populus* L.) have the capacity to resprout, but this trait is far less common in gymnosperms (McDonald and Tappeiner 1996, Bond and Van Wilgen 2012). Resprouting is often viewed as an adaptation to high-severity fire (Clarke et al. 2013b, Pausas et al. 2016), although resprouting can occur following other disturbances such as drought or grazing (Zeppel et al. 2015). Because resprouting allows plants to take advantage of surviving tissues (e.g., roots, lignotubers), recovery of the individual may be relatively rapid and less uncertain compared to regeneration from seed. Recovery times may also be influenced by the position of the resprouting buds (below-ground, basal, or aerial); species that maintain epicormic buds on the existing skeleton of the main stem may recover forest structure and function more rapidly compared to basally resprouting species (Pausas and Keeley 2017), assuming the buds are not damaged by the disturbance. Large, high-severity disturbance can thus shift species composition toward dominance of sprouting species if these species are present prior to disturbance (§3.4, Recovery: *Competitive effects and community interactions*).

In crown-fire ecosystems there are many examples of persistence through resprouting. Basal resprouting is widespread in fire-prone shrublands throughout the world (Keeley et al. 2011a) as well as shrubs and small trees that form forest understories (Fig. 3a), whereas epicormic resprouting along the stems of burned trees is less widely distributed (Pausas and Keeley 2017). Epicormic resprouting arises from latent buds along tree stems that are typically protected by thick bark, although in some *Eucalyptus* they are embedded in the woody tissues beneath relatively thin bark. The primary distinction between these two modes is that basal resprouting allows for persistence of the genet, whereas epicormic resprouting ensures persistence of individual ramets. The latter facilitates retention of the arborescent skeleton, thus allowing for rapid recovery under recurrent high intensity fires (Collins 2020). Indeed, certain *Eucalyptus* species exhibit over 99% epicormic resprouting, such that the forest recovers relatively rapidly to its original composition and structure (Fig. 3b). In most temperate forests, we generally think of crown fires as stand-replacing events where recovery is primarily from reproduction, but in certain Australian forest types, as well as North American and European forests dominated by *Quercus* and other resprouting broadleaved trees, even crown fires are not stand-replacing; rather, the individual trees persist. This is in contrast to

**Fig. 2.** Anatomical adaptations to resisting effects of fire include (a) lifted crowns (*Pinus ponderosa* Douglas ex D. Lawson, Valles Caldera National Preserve, New Mexico, USA, and (b) thick heat-resistant bark in *P. sylvestris* L., Mongolia). Photos: PM Brown, Rocky Mountain Tree-Ring Research.

*Pinus* in the Northern Hemisphere, where the resprouting strategy is almost unknown (although there are notable exceptions, e.g., *Pinus canariensis* C. Sm. Ex. D.C. (Pausas and Keeley 2017)).

Counterintuitively, many woody plants subject to crown-fires lack resprouting traits for persistence. In those species commonly associated with crown-fire regimes, such as lodgepole pine (*Pinus contorta* Douglas), this is perhaps not unexpected since resprouting is a rare trait in the genus. However, within Mediterranean-climates, most shrublands that are dominated by angiosperm shrubs include entire clades that lack the capacity for persistence through resprouting, and there is evidence that this is a derived trait (Keeley et al. 2011a). This is surprising since basal resprouting is nearly ubiquitous in woody angiosperms (Wells 1969). Hypotheses for this loss of persistence center on the capacity to adapt to new climates through increased number of sexual generations, and on ecological effects, e.g., resprouts may also increase competition with new seedlings (Keeley 2012). Considering the widespread distribution of resprouting capacity, it likely represents a persistence strategy in response to multiple forms of disturbance, including intense browsing or extreme climatic events including freezing and drought (Keeley et al. 2011a).

### 2.2. *Individual tree persistence: Drought*

Drought is a common ecosystem disturbance, and most climate change models suggest a future of increasingly severe droughts worldwide (Trenberth et al. 2014). The ecological impacts of drought (an extended period of unusually low rainfall, leading to shortage in soil moisture) are exacerbated by elevated temperatures, leading to the “warm drought” syndrome that is becoming increasingly pervasive (Lloret and Batllori 2021). Extreme droughts can alter community composition through differential survival, which is well documented worldwide for both angiosperms and gymnosperms (McDowell et al. 2008), especially in arid and semi-arid ecosystems. During the 1950s a severe drought in the semi-arid southwest U.S. resulted in a 2 km shift in the distribution of ponderosa pine, which was replaced by more drought tolerant piñon-juniper woodland (Allen and Breshears 1998). Such rapid climate-driven shifts occur mostly by differences in persistence; during this episode, the ecotone shift was driven largely by mortality of ponderosa pine compared to persistence of piñon and juniper. On a similar landscape during a 15-month drought between 2002 and 2003, the piñon-juniper community was altered dramatically by mortality of more than 90% of the dominant tree, *Pinus edulis* Engelm., whereas 75% of the associated *Juniperus monosperma* (Engelm.) Sarg. survived (Breshears et al. 2005).

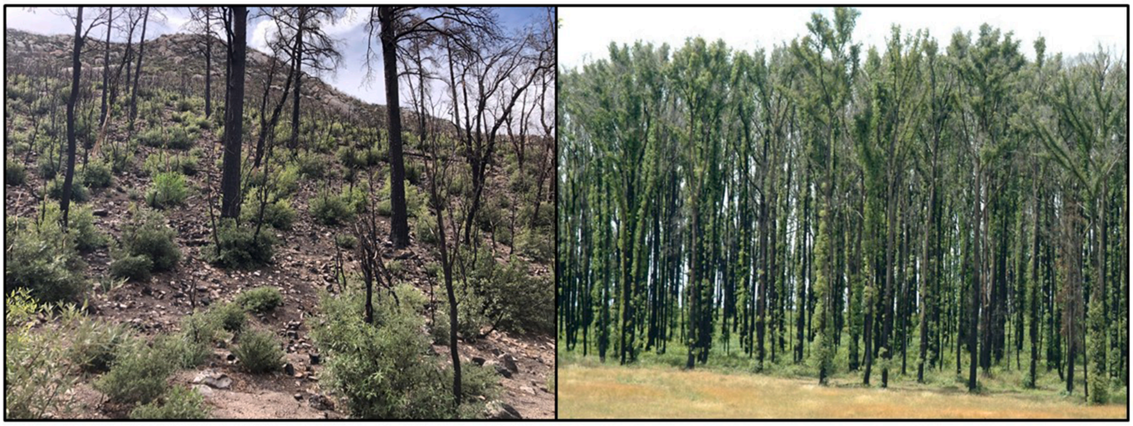


**Fig. 3.** A. Silverleaf oak (*Quercus hypoleucoides* A. Camus) basal resprouting 1 year after 2020 Bighorn Fire, Coronado NF, Arizona, USA. Photo JR Malusa, University of Arizona. B. Epicormic resprouting in *Eucalyptus* L'Her. 11 months after the 2009 Victoria fires. Photo: JE Keeley.

Persistence during severe droughts is highly dependent on characteristics of the plant hydraulic system (Choat et al. 2018). Within the same plant community, coexisting woody species commonly have diverse hydraulic strategies, and as a consequence may express different patterns of persistence during severe droughts (Johnson et al. 2018). The ecological and physiological effects of drought *per se* (precipitation anomalies) also interact strongly with changes in temperature regimes; warmer droughts are more likely to induce widespread mortality than droughts that occur under normal temperatures (Adams et al. 2009, McDowell 2011), although mechanisms remain a matter of debate (Sala et al. 2010, Anderegg et al. 2012).

Woody plants prevent desiccation injury by xylem transport of water from the roots, but xylem fluid under tension is vulnerable to sudden shifts from water to gas; these air bubbles block water transport in the xylem, a process known as *cavitation* (Davis et al. 2002, Maherali et al. 2004). Adaptations to drought revolve around avoiding embolism by anatomical features of the xylem cell and porosity of cell walls. Resistance to cavitation is a key determinant of persistence in the face of severe drought (Vilagrosa et al. 2012). Stomatal conductance, rooting depth and cellular osmotic conditions are also key plant functions that determine drought persistence (Markesteijn et al. 2011).

Understanding mechanisms of tolerance to drought is complicated by the range of plant hydraulic strategies for dealing with this stress. Even in the absence of catastrophic failure in water transport, persistence can be threatened by changes in carbohydrate reserves necessary for respiratory function and osmotic regulation (Hammond et al. 2019, Sapes et al. 2021). Many plants regulate water loss by stomatal closure, which reduces water loss but also limits carbon uptake necessary for photosynthesis and Calvin cycle processes that convert $CO_2$ to glucose via carbon fixation and reduction reactions. Reduced xylem flow also reduces a key tree defense against insects, leading to increased vulnerability to these mortality agents (Bentz et al. 2010, Huang et al. 2020).

Plant functional traits play a key role in determining persistence through severe drought, which can confer different advantages dependent on the pattern of drought (Trugman et al. 2020). McDowell et al. (2008) proposed a model explaining persistence patterns in the context of different water use strategies in ways that affect carbon balance and pathogen resistance. Although water use strategies comprise a continuum within and among species, their model suggests different outcomes for isohydric *vs.* anisohydric strategies in the face of different patterns of drought. Isohydric strategies maintain constant leaf water potentials by regulating stomatal conductance, whereas anisohydric plants maintain high stomatal conductance in the face of diminished leaf water potentials (Sade et al. 2012). Associated with these strategies are differences in water availability due to rooting depth, and cellular tolerance to desiccation through osmotic adjustments.

There is circumstantial evidence that global warming is changing persistence traits resulting in coordinated shifts toward communities with more drought-tolerant traits driven by selective mortality (Trugman et al. 2020, Roos and Guiterman 2021). Global warming is altering fire regimes in the North American boreal forest (Kelly et al. 2013), resulting in increased drought impacts that are changing plant assemblages, moving conifer forests to broadleaf deciduous forests (Keeley and Pausas 2019). However, drought is a broad term that is quantified by over 100 different indices to describe its properties and impact (Zargar et al. 2011). With respect to plant communities, there are species-specific differences dependent on the pattern of drought, and traits favorable for persisting in the face of short-term extreme droughts may differ from traits favoring persistence in the face of long-term droughts. The primary mechanisms of drought-induced tree mortality, carbon starvation (resulting from stomatal closure) and hydraulic failure, vary widely across taxa (Adams et al. 2017). Loss of xylem hydraulic conductivity is the most prevalent cause of mortality, although simultaneous loss of carbon reserves is widespread, particularly in gymnosperms (McDowell and Sevanto 2010). Selection may increasingly favor traits that confer the capacity to maintain plant hydraulic function, photosynthesis, and non-structural carbohydrate reserves during periods of low productivity, and mechanisms to maintain resistance biotic stressors such as insects and pathogens (McDowell et al. 2008).

## 3. Mechanisms of recovery

If persistence mechanisms are overcome, vegetation *recovery* is the next potential pathway of ecological resilience. Recovery represents the replacement of the pre-disturbance population through recruitment or colonization; thus, recovery processes occur at the level of populations (Fig. 1). The post-disturbance period is a critical stage in community development, during which the persistence and coexistence of multiple species is determined in part by life history adaptations to the unique properties of such environments (the ‘regeneration niche’, *sensu* Grubb (1977)). Recovery processes determine the initial density, establishment success, and survivorship of recruits. For example, how propagules or recruits arrive at sites following disturbance is of critical importance for recovery processes, whether from a persistent seed bank, or via seed dispersal (Bond and Van Wilgen 2012; Pausas and Keeley 2014, 2017). Understanding the mechanisms that underly recovery strategies is essential to assessing the potential for resilience following major disturbances.

### *3.1. Seed banks, serotiny, and advance regeneration*

Populations may not be solely dependent on the survivorship of reproductive individuals, but may rely instead on the survivorship of seeds or propagules. Seeds that are developed and stored in the soil or other protected structures (e.g., closed arboreal cones) prior to disturbance represent an *in situ* seed bank, allowing for recovery of populations without the need for dispersal from surviving individuals elsewhere. A large literature has been developed around the dynamics of soil seedbanks (Leck 2012, Saatkamp et al. 2014). Although few conifer species have persistent (longevity $>$ 1 yr) soil seedbanks, soil seed banking is common in many other taxa, especially among angiosperm shrub, grass, and forb species (Knapp et al., 2012; USDA-US Forest Service, 2021). The availability of soil-stored seed following disturbance can allow a variety of plant functional types to dominate previously forested post-fire landscapes rapidly, at least initially. Some shrub and herbaceous species exhibit seedbank-mediated adaptation to disturbance, such as smoke- (Keeley 1997, Abella 2009) and heat-induced germination (Keeley and Keeley 1987) of seeds that otherwise remain dormant in soil.

As an alternative to soil seed banking, some conifer species possess aerial seedbanks (Fig. 4). A common mode of aerial seed banking is serotiny, in which trees store viable seeds in closed cones for one to many years and release them following disturbance, even when that disturbance kills the adult trees (Schwilk and Ackerly 2001). Serotiny in response to fire appears across many unrelated taxa (Bond and Van Wilgen 2012). Some conifer species that are not generally serotinous may display facultative serotiny if a fire burns in the late summer or fall, when cones have matured, and kills the tree but does not destroy its seeds (Larson and Franklin 2005, Pounden et al. 2014). Relative to species that rely on residual live reproductive individuals to disperse seeds into a disturbed site (§3.2: *Dispersal*), serotinous species are well adapted to recruit following large disturbances with extensive high-severity patches (Turner et al. 1997). Large high-severity wildfires can thus shift composition in favor of serotinous species (Donato et al. 2009, Hansen et al. 2018).

Under some circumstances, large, mature individuals may be killed by disturbance while small, immature individuals survive. The surviving juvenile cohort functions as advance regeneration and may allow for relatively rapid recovery (Greene et al. 1999). Advance regeneration may be particularly important following drought, windstorms, or pest outbreaks where mortality may be concentrated in large individuals (Kayes and Tinker 2012, Redmond et al. 2018). Because advance

**Fig. 4.** Post-fire reproduction of serotinous species. Left: knobcone pine (*P. attenuata* Lemmon), Mendocino National Forest, California USA. Photo: DJN Young. Right: interior Lodgepole pine (*P. contorta* var. *latifolia* Engelm.), following 2016 Cold Springs Fire, Arapaho-Roosevelt NF, Colorado, USA. Photo: C Rhoades, Rocky Mountain Research Station, US Forest Service.

regeneration becomes established in the forest understory prior to disturbance, it is often enriched in shade-tolerant species, which may lead recovering communities to be similarly enriched in such species (Kayes and Tinker 2012, Young et al. 2020a).

### 3.2. Dispersal

Seed dispersal is of critical importance for obligate seeding species that do not create persistent seed banks. Recovery in ecosystems dominated by these species in disturbed sites generally depends on wind or animal dispersal of seeds into the site from nearby surviving reproductive trees (McCaughey et al. 1986) (Fig. 5).

The influence of seed source proximity on seed input has been confirmed by numerous empirical studies of post-fire seedling recruitment patterns, which, for non-serotinous species, consistently find a strong negative relationship between tree seedling density and distance to the nearest surviving reproductive tree(s) or low-severity/unburned patch (Donato et al. 2009, Welch et al. 2016, Owen et al. 2017, Stevens-Rumann and Morgan 2019, Stewart et al. 2021). Most conifer seeds are initially wind-dispersed and exhibit relatively limited dispersal distances; the majority of species studied disperse seeds $< 50–75$ m (Burns and Honkala 1990, Greene et al. 2004, Bonnet et al. 2005, Rother and Veblen 2016, Halpern and Antos 2021) (Figure S-1), although longer-distance dispersal does occur, often aided by secondary dispersal by rodents or birds (Vander Wall 1992, 2008).

Short dispersal distances may be beneficial in the context of historic high-frequency, low-severity disturbance regimes that produce spatially heterogeneous mortality patterns, such that few high-mortality areas are far from residual reproductive trees (Safford and Stevens 2017). In contrast, the increasingly common large patches of high-severity area lie

**Fig. 5.** Dense post-disturbance *P. ponderosa* seedling recruitment. Monument Canyon Research Natural Area, Santa Fe National Forest, NM. Photo: DA Falk.

beyond the reliable dispersal range of the nearest surviving reproductive trees (Tautenhahn et al. 2016, Stevens et al. 2017a, Steel et al. 2018, Falk et al. 2019). However, fires that burn large areas of forest at high severity do not necessarily create completely dispersal-limited patches. Many large fires are spatially heterogeneous, leaving a patchy distribution of surviving trees that can serve as seed-source islands in post-fire landscapes (Fig. 6). Patches of surviving trees (*fire refugia*) may play an important role in determining recovery in many coniferous forests (Turner et al. 1998, Coop et al. 2019).

Infrequent long-distance dispersal may be an important mechanism behind tree population expansion (Allen 1987, Clark 1998, Clark et al. 1998). Birds may play a keystone role in long-distance seed dispersal of certain conifer species, such as dispersal of *Pinus albicaulis* Engelm. seeds by Clark's nutcrackers (*Nucifraga columbiana* Wilson) (Williams et al. 2020). While substantial long-distance (e.g., >200 m) dispersal is relatively rare for western U.S. dry forest tree species, it is sometimes recorded. For example, Kemp et al. (2016) estimated the probability of observing at least one non-serotinous conifer seedling in a 600 $m^2$ area 300 m from the nearest seed source more than 10 years following fire to be approximately 20%. However, even a 300-m dispersal range is short relative to the scale of contiguous high-severity patches spanning more than 2 km in the shortest dimension in many recent large wildfires (Eidenshink et al. 2007) (Fig. 6). Shade-tolerant conifer species (e.g., true firs, *Abies* Mill spp.) tend to have smaller seeds and longer dispersal ranges than shade-intolerant species such as pines (McCaughey et al. 1986, Burns and Honkala 1990), so sites far from residual forest may receive seed rain more heavily dominated by shade-tolerant species. Within conifers, seed size tends to be larger for species with animal-dispersed seeds compared to those with seeds dispersed primarily by wind (Leslie et al. 2017), but animal dispersed species may be able to more easily colonize large, high severity patches in post-fire landscapes. In the case of *Pinus albicaulis,* animal dispersal of seeds into post-fire landscapes may be key to its ability to persist under historical fire regimes (Keane et al. 2012).

Conceptually, seed input should depend on not only the proximity of seed sources but also their density and spatial pattern (Greene and Johnson 1996, Clark et al. 1999, Peeler and Smithwick 2020). Empirical approaches that incorporate seed source density and/or spatial arrangement into seed availability metrics also detect the expected relationship between seed source density and seedling recruitment (Shive et al. 2018, Stewart et al. 2021), further supporting the idea that recovery from more spatially heterogeneous disturbances may be more likely and/or rapid (Haire and McGarigal 2010, Tepley et al. 2017). The generally high spatial heterogeneity associated with drought-related mortality may also help to explain the high densities of seedlings sometimes found following drought-related mortality events (Young et al. 2020a, Fettig et al. 2019), as could instances where seed production is unaffected during drought (Wright et al. 2021); alternatively, these seedlings may largely represent advance regeneration. Other spatially heterogeneous drought-related mortality events in areas with presumably little advance regeneration have not exhibited substantial post-drought seedling recruitment (Allen and Breshears 1998).

When disturbed areas are beyond the scale of long-distance dispersal, large disturbed patches may be re-colonized over time by multiple successive generations of trees, each reaching maturity before dispersing seeds further into the patch (Falk et al. 2019). In a severely burned patch approximately 500 m wide, Nagel and Taylor (2005) observed trees that recruited in the center of the patch were on average 22 years younger than trees recruited near the edge of the patch; similarly, Schwilk and Keeley (2006) observed a decrease in mean age of *Pinus sabiniana* Douglas ex D. Don recruits with distance from a fire refugium. Similar recruitment patterns have been observed in conifer invasions of grasslands and alpine meadows (Coop and Givnish 2007, Halpern et al. 2010). In these ecosystems conifer invasions may subsequently change microenvironments and fuel composition, discouraging fire and promoting further invasions (Engber et al. 2011). These observations are consistent with progressive multi-generational recruitment into burned areas, although they are also consistent with initial tree reestablishment, and exclusion of later recruits, where seed rain is strongest.

### 3.3. Germination, seedling survivorship, and growth

After seeds arrive at a site, they must germinate, and seedlings must establish and grow, for forest recovery to proceed (Harper 1977, Dobrowski et al. 2015). Many conifer species—especially, but not exclusively, shade-intolerant pines—establish more successfully on bare mineral soil than on litter-covered soil (Gray and Spies 1997, Safford and Stevens 2017). Therefore, the potential for seed rain to translate into

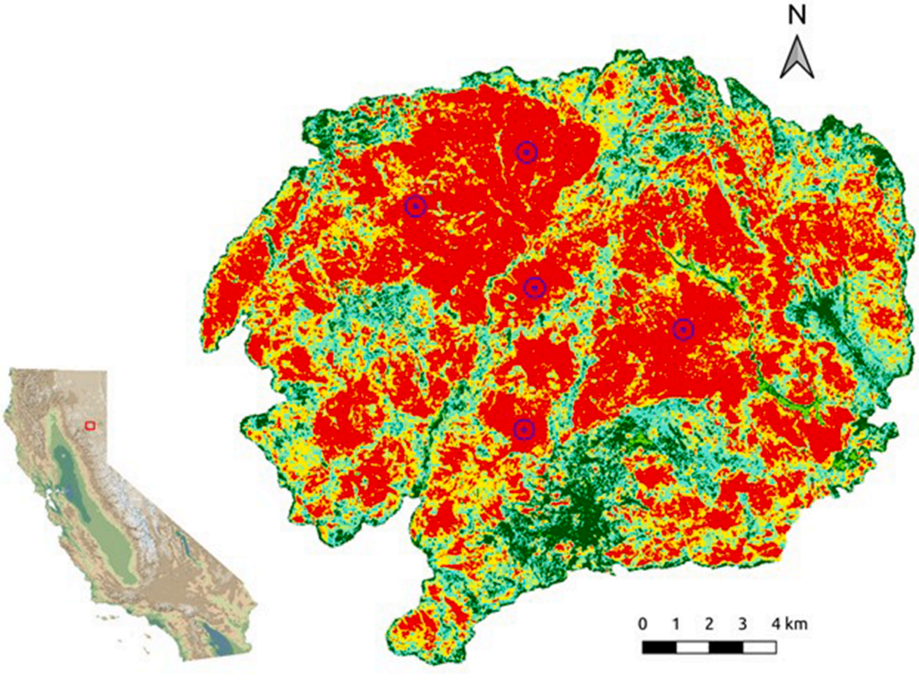


**Fig. 6.** Severity map of the 2007 Moonlight Fire, Plumas National Forest, California, USA. Severity is indicated by colors: red indicates high severity (75–100 % overstory mortality); yellow, light and dark green indicate moderate, low, and unburned areas respectively within the fire perimeter. The five pairs of concentric circles show dispersal radii of 60 m and 300 m around 5 hypothetical residual trees. The inset map shows the location of the severity map within the state of California. Severity map from MTBS (www.mtbs.org). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

forest recovery will depend partially on the type of disturbance: for example, fire may consume litter and duff layers, leaving mineral soil exposed (although also vulnerable to surface erosion), while drought-related overstory mortality is often associated with additional litter deposition.

Following successful germination (or resprouting) after disturbance, survivorship and growth of juvenile plants are particularly sensitive to environmental conditions. Seedling establishment following disturbance tends to be more limited closer to the arid extremes of forest and/or tree species distributions (Rodman et al. 2020, Stewart et al. 2021), although fine-scale climatic and topographic refugia such as those afforded by woody debris can ameliorate otherwise harsh conditions and promote seedling recruitment (Dobrowski et al. 2015, Owen et al. 2020, Marsh et al. 2022). Weather in the years immediately following disturbance can also strongly influence forest recovery (Littlefield et al. 2020). The effects of short-term post-disturbance climatic stress are corroborated by numerous studies that find reduced post-fire conifer recruitment under unusually hot and/or dry post-fire conditions (Harvey et al. 2016, Urza and Sibold 2017, Stevens-Rumann et al. 2018, Davis et al. 2019, Hansen and Turner 2019, Young et al. 2019, Stewart et al. 2021). Low-elevation forests in the western U.S. are increasingly experiencing years in which weather conditions do not meet minimum thresholds for successful forest regeneration (Fig. 7) (Stevens-Rumann et al. 2018, Davis et al. 2019). Tree species recovery in the context of weather and climate variation is constrained by the dependence of tree regeneration on seed rain from the residual reproductive trees (Young et al. 2019). When post-fire weather and climate do not match the requirements of the available seed, the system may be vulnerable to reorganization.

### 3.4. *Competitive effects and community interactions*

Successful recovery is determined partially by the capacity of recruits to compete for resources within the post-disturbance community. In ecosystems with strong post-disturbance shrub growth and poor initial conifer regeneration, sites often become dominated by shrubs and remain so for decades (Russell et al. 1998, Lauvaux et al. 2016). Comparable self-reinforcing dynamics have been observed in shrublands that have been invaded by exotic grasses (Keeley and Brennan 2012). Nonetheless, continued seed dispersal and seedling recruitment over time may allow for delayed recovery. Tree seedling establishment is often observed over at least a 10-year period following fire (Harvey et al. 2016, Stevens-Rumann et al. 2018, Davis et al. 2019) and sometimes over multiple decades (Nagel and Taylor 2005, Savage and Mast 2005, Haire and McGarigal 2010, Lauvaux et al. 2016), even when little recruitment was observed in the first 10 or more years (although other studies have found regeneration pulses limited to the first 3–10 years post-fire (Tepley et al. 2017, Urza and Sibold 2017, Davis et al. 2019). Long-term recruitment may be particularly important for recovery in sites far from seed sources, as multiple years of low-density, long-distance seed rain may accumulate to support meaningful tree establishment that lags behind sites closer to seed sources (Turner et al. 1998, Haire and McGarigal 2010). Delayed (e.g., >10-year post-disturbance) tree recruitment appears more often in shade-tolerant species (Nagel and Taylor 2005, Lauvaux et al. 2016), likely due to the need for establishing trees to tolerate competition from other vegetation that establishes in the intervening years (Tepley et al. 2017, Werner et al. 2019, Tubbesing et al. 2021).

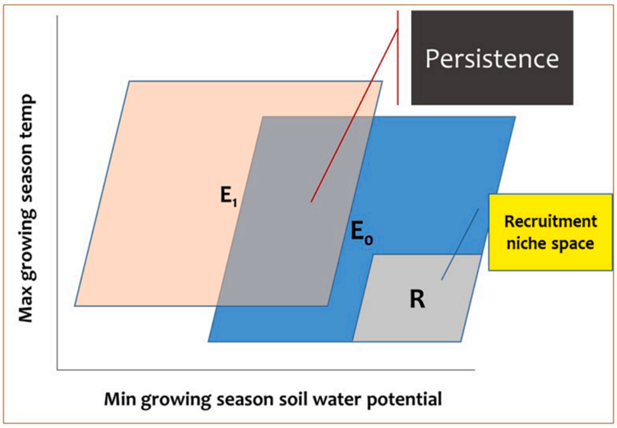


**Fig. 7.** Climate space for the persistence and recruitment niches, in axes of minimum growing season soil water potential and maximum growing season temperature. The climate space for established trees (*$E_0$*) is broader than the recruitment niche (*R*), which is limited to the cooler, more mesic conditions within *$E_0$*. Projections of future climate (*$E_1$*) are moving toward warmer, drier conditions, potentially problematic for seedling and sapling growth stages.

Despite the potential for delayed forest establishment far from seed sources, regeneration is likely to become increasingly difficult as competing vegetation (often shrubs) becomes established over time (Fig. 8). This may explain why some studies find the strongest pulse of recruitment relatively soon after disturbance (Harvey et al. 2016, Tepley et al. 2017, Urza and Sibold 2017, Davis et al. 2019). For example, following fire in dry coniferous forests of the southwestern U.S., vigorously resprouting Gambel oak (*Quercus gambelii* Nutt.) shrubs may outcompete *P. ponderosa* Douglas ex D. Lawson seedlings for light and water, limiting their capacity for recovery (Guiterman et al. 2018). In areas where trembling aspen (*Populus tremuloides* Michx.) co-occurs with conifer species, aspen often initially dominates the recovering tree community, likely a consequence of its resprouting ability, but over subsequent decades composition generally shifts toward conifer dominance due to their relative juvenile shade tolerance and greater adult height and longevity; this constitutes a *transient reorganization* (Fig. 9) (Smith and Smith 2005). A wide range of other perennial early successional species have been observed to dominate landscapes in the years initially following fire, including bracken fern (*Pteridium aquilinum* (L.) Kuhn); whitethorn, deerbrush, and buckbrush (*Ceanothus* L. spp.); New Mexico locust (*Robinia neomexicana* A. Gray); bigleaf maple *(Acer macrophyllum* Pursh.) and others. High-severity fire may facilitate invasions of native and exotic ruderal species, which may lead to self-reinforcing changes in community composition and fire hazards (Keeley and Brennan 2012, Coop et al. 2016). However, in some cases topoclimate (e.g., aspect, elevation) may be more important than cover of competing vegetation for predicting regeneration success following fire (Rother and Veblen 2016). Transient vegetation communities may also alter fire regimes, encouraging further vegetation change (e.g., Engber et al. 2011).

The preceding sections highlight the capacity of species to recover from disturbance. However, recent literature suggests that recovery is becoming more difficult under current conditions in many ecosystems regardless of species adaptions to disturbance regimes (Fairman et al. 2019, Davis et al. 2019, Turner et al. 2019). If a population's capacity to recover from disturbance is overwhelmed, the next phase of resilience is community reorganization.

## 4. Reorganization

When mechanisms of persistence have been overcome, and recovery processes fail or are compromised, an ecological system will reorganize. Ecological reorganization can take a wide variety of forms, from temporary shuffling of species dominance relationships, to persistent type conversion involving major changes in plant functional types (Fig. 1) (Falk et al. 2019, Keeley et al. 2019, Steel et al. 2021). Individual disturbance events, or interactions between two or more disturbances, may act as triggers for abrupt change; however, the ecosystem is unlikely to persist in the alternative state unless subsequent disturbances, climate, or plant-disturbance interactions function as an equilibrating force to promote stability of the new state, while limiting the potential to

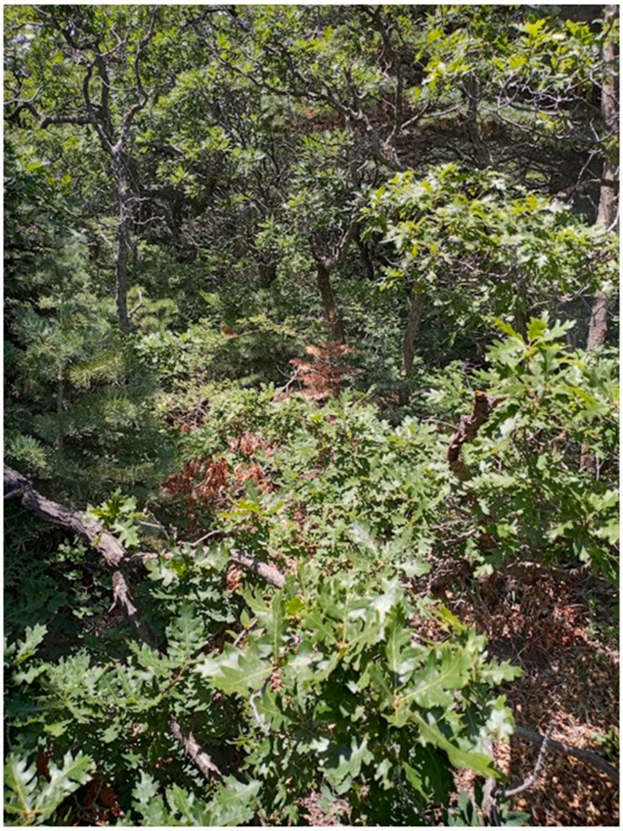


**Fig. 8.** Intense competition may inhibit successful establishment of prior dominant species. Dense post-fire *Quercus gambellii* Liebm. thicket, Sandia Mountains, Cibola National Forest, NM, USA. Photo: DA Falk.

return to the previous condition or transition to another state.

*Observations and definition:* Reorganization (referred to variously as realignment, ecosystem transition, transformation and conversion (van Mantgem et al. 2020a)) is expressed in changes at the community level along a spectrum of magnitude. In some cases, reorganization consists primarily of changes in relative abundance of existing species in the community; these changes can be transient, or they can represent a persistent vegetation shift (Barton and Poulos, 2018). More extensive reorganization can involve turnover in community composition, structure, and physiognomy, as when new species enter the community, and other formerly present species are eliminated (Fig. 10). More fundamental forms of reorganization are expressed by a change in dominant plant functional types, such as forest-shrub, forest-grass, or shrub-grass conversions (Guiterman et al. 2018, Batllori et al. 2020, Armenteras et al. 2021). Vegetation type conversion (VTC) is notable as a special case of reorganization in which the change in community type and dominant plant functional types are extensive, and the alternative state is persistent and reinforced by novel interactions among climate, vegetation, and disturbances.

*Time scales:* There is no single time threshold at which reorganization is delineated; indeed, the multiple expressions of reorganization can progress at different rates (Falk et al. 2019). On centennial to millennial and longer time scales, reorganization occurs in response to changing climate; in this context it is understood as an inherently adaptive Earth system process expressed over the history of life (Jackson and Overpeck 2000, Pausas and Keeley 2009, Keeley 2012). On shorter ecological time scales (years to centuries), reorganization is more likely to be driven by disturbance events, episodes of extreme climate (droughts or heat waves), or other triggering events (Ruthrof et al. 2018).

To understand the mechanisms that drive ecological reorganization, we examine the following questions: (1) What ecological changes constitute reorganization, and which factors drive these changes across time scales? (2) What are the mechanisms and ecological dynamics of reorganization? (3) What factors (external drivers and internal feedbacks) reinforce these changes, causing them to persist as alternative

**Fig. 9.** Shade-tolerant conifer recruitment in the understory a century after stand-replacing fire, indicating transient reorganization. The overstory is currently dominated by aspen (*Populus tremuloides* Michx.) that initiated post-fire from basal sprouts. San Francisco Peaks, Coconino NF, Arizona, USA. Photo: DA Falk.

**Fig. 10.** Observations of post-fire ecological reorganization with varying degrees of persistence involving plants of four different functional groups: (upper left) dense post-fire growth of bracken fern (*Pteridium aquilinum* (L.) Kuhn) 9 years post-fire in a previous mixed-conifer stand, Chiricahua Mountains, Coronado NF, Arizona, USA. Photo: DA Falk; (upper right) bunchgrass post-fire dominance of previous dry conifer stand 9 years post-fire, Chiricahua Mountains, Coronado NF, Arizona, USA. Photo: DA Falk; (lower left) *Ceanothus velutinus* Douglas dominance of former mixed-conifer forest 11 years after the 2007 Moonlight Fire, Plumas NF, California, USA. Photo: DJN Young; (lower right) conversion of conifer (Douglas-fir, white fir) forest to mixed species hardwood-shrub dominated forest, Klamath NF, California, USA 14 years after the 2001 Happy Camp Complex. Photo: AJ Tepley.

metastable states instead of transient successional change?

### *4.1. Observations: Where is ecosystem reorganization being observed and documented?*

Ecosystems are inherently dynamic, so the observation of change over space and time does not necessarily indicate that a system is reorganizing permanently or uncharacteristically. The study of seral ecology was foundational to the development of modern ecological theory, including species interactions and community assembly rules (Whittaker 1960, Chase 2003). One of the earliest debates in ecology concerned mechanisms and temporal patterns of post-disturbance succession: Clements (1936) argued that plant communities are holistic and essentially integrated entities in which succession is an orderly and well-regulated process analogous to an organism healing to return to its canonical state, whereas Gleason (1926) contended that communities are transient associations among species acting individualistically. These arguments are surprisingly relevant today as we consider the emergent patterns and mechanisms of ecosystem reorganization.

*Gradual reorganization in response to changes in mean conditions.* Evidence of ecosystem reorganization is a salient feature in the paleoecological record (Iglesias and Whitlock 2020), reflecting recombination and reorganization of ecological communities as species ranges shift due to changes in climate (Colwell and Rangel 2009, Jackson and Blois 2015, Crausbay et al. 2017, Fernandez et al. 2021). Processes of ecosystem transformation driven by climatic variation continue into the present, and are likely to accelerate under projected future climate change scenarios (Parmesan 2006, Nolan et al. 2018). Superimposed on background processes of climate-driven ecosystem reorganization, we may expect anthropogenic activity to promote or alter trajectories and rates of reorganization through anthropogenic climate change and other global change pressures including landscape fragmentation, human alteration of disturbance regimes, altered global biogeochemical cycles, and proliferation of non-native species that alter disturbance-feedback dynamics (Dale et al. 2001, Jackson et al. 2009, McWethy et al. 2010, Falk 2017).

While community change in the paleoecological record may seem less relevant to understanding ecological resilience today, there is no clear line that divides the processes or mechanisms at work. Reorganization can (and does) occur over decadal and longer time scales, through demographic processes and turnover in species composition, even without abrupt episodes of mortality, reflecting the inherent inertia of plant communities (Westman 1978, Erikkson 1996, Lloret et al. 2012). Expressed changes in species distributions reflect changes in the ratio of colonization to extinction at the leading and trailing margins of a species range (Loarie et al. 2009). When the rate of climate change exceeds species dispersal rates, lags or disequilibria may occur in species ranges (e.g., where long-lived adults persist after the climate has become unsuitable for new seedling establishment of the same species). This ecological inertia creates lags in local extinction and colonization that over time determine the trajectory of species turnover and community change on the landscape (Webb 1986, Jackson and Sax 2010, Talluto et al. 2017). Extinction debt represents local persistence with population vital rates below replacement, resulting ultimately in recruitment failure and local extirpation. In contrast, colonization credits occur in unoccupied locations fitting existing niche requirements, as well as areas open for some species in the regional pool potentially better adapted to emerging climate. Ultimately, changes in fundamental demographic parameters (birth, immigration, death, and emigration) underlie all shifts in species distributions. There is abundant evidence of climate-driven species range shifts leading to community reorganization (Chen et al. 2011), reflecting the species-individualistic nature of community organization. Contemporary observations are largely associated with accelerated shifting of climatic zones in relation to species niche space

(Colwell and Rangel 2009, Thomas 2010, Hannah et al. 2014, Shirk et al. 2018). It is likely that similar processes have been at work for millions of years as species have adapted to changing climate.

*Reorganization in response to the loss of formerly frequent disturbance.* Reorganization can proceed along different time scales beyond gradual reorganization in response to changing climate. Ecosystems can reorganize rapidly in response to the elimination or a reduced frequency of an ecosystem's characteristic disturbances. In some regions, wildfire area burned has been decreasing due to human fire suppression and landscape fragmentation (Andela et al. 2017). Such changes would be most consequential for communities in which characteristic wildfire plays a stabilizing role in community structure and composition (Parsons and DeBenedetti 1979, Binkley 2021). For example, reduction in the frequency of burning in dry oak and oak-pine forests of eastern North America led to increases in the abundance of mesophytic species (e.g., maples, beech, ashes, and basswood); increasing abundance of these species in turn altered forest microclimate and fuel characteristics, producing a self-perpetuating feedback that made the forests less conducive to fire and more favorable to the persistence of these species at the expense of oaks and pines (Nowacki and Abrams 2008, Kreye et al. 2013, McDaniel et al. 2021).

In drier western North American conifer forests, exclusion of fire has led similarly to changes in community composition, *viz.* increased abundance of shade-tolerant species such as white fir, *Abies concolor* [Gordon & Glend.] Lindl. ex Hildebr. (Dolanc et al. 2014). These changes have made forests more prone to high-severity fire, and increasingly vulnerable to drought-induced mortality (Earles et al. 2014, Restaino et al. 2019). Because these shade-tolerant conifers typically have longer seed dispersal distances than their shade-intolerant counterparts, they may be better suited to re-establish and become dominant in large patches of high-severity fire. For example, shade-tolerant conifers or drought-tolerant oaks have become more abundant in many formerly ponderosa pine and dry mixed-conifer forests. In a southwestern Sky Island forest, O'Connor et al. (2017) found a shift from disturbance-adapted species to competition- and productivity-mediated recruitment as fire intervals increased beyond the historical mean.

Reduction in fire frequency can also lead to type conversion of savannahs and grasslands to shrubland or closed forest (Bond 2019). The high flammability and rapid post-fire recovery of grasses puts them at an evolutionary advantage over woody vegetation in systems that are exposed frequently to fire (annually to every few years); human-driven reductions in burning have led to woody plant encroachment in many of these systems globally (Luger and Moll 1993, Ratajczak et al. 2012, Stevens et al. 2017b). Restoring fire regimes can thus play a key role in maintaining the spatial extent and ecological functions of grass-dominated and savannah ecosystems (Smit et al. 2010).

*Rapid reorganization in response to novel disturbance.* Unlike decadal range shifts driven by climate, many observations of ecosystem reorganization represent *abrupt change*, especially when triggered by disturbance episodes that are larger, more severe, or occur more frequently than background temporal variability (Ratajczak et al. 2018, Jentsch and White 2019, Turner et al. 2020). Among the most common triggers of abrupt change in terrestrial systems are wildfires (Holz et al. 2015, Hansen et al. 2021), heat waves and episodes of extreme drought (Batllori et al. 2020, Senf et al. 2020), and insect outbreaks (Weed et al. 2013, Kautz et al. 2017). In some cases, combinations of two or more stress or disturbance types, or a sequence of successive disturbances, may drive more substantial change with greater potential to persist compared to that expected from individual disturbances (Batllori et al. 2019). Abrupt ecological change may also reflect the cumulative effect of other factors that have been at work for much longer periods, such as decades of invasion by non-native species that create the conditions for a tipping point event.

Conversions from forest to shrubland or grassland, or from shrubland to grassland, are among the most widely observed type conversions on contemporary landscapes following severe wildfire and drought (Walker et al. 2018). Globally, approximately one-quarter of forest loss is attributable to wildfire (Curtis et al. 2018), a trend that is likely to increase as fire severities (van Mantgem et al. 2018, Singleton et al. 2019, Parks and Abatzoglou 2020), sizes (Westerling 2016), and area burned (Abatzoglou and Kolden 2013, Kitzberger et al. 2017) increase under the influence of changing climate and fuel accumulation. As climate simultaneously becomes less favorable to tree establishment (Savage et al. 2013, Rother and Veblen 2016, Tepley et al. 2017), wildfires are likely to trigger widespread ecosystem conversion.

Reorganization also may occur in response to introductions of non-native plants, insects, or pathogens. In deciduous forests of eastern North America, where tree species diversity tends to be higher than western conifer forests, several former canopy dominants have been lost or converted to short-lived, smaller trees by invasive insects and pathogens introduced over the last century (e.g., American chestnut due to the chestnut blight, American elm due to Dutch elm disease, ash species due to emerald ash borer). In the late 20th to early 21st century, the hemlock wooly adelgid (*Adelgis tsugae* Annand) drove extensive mortality of eastern hemlock trees throughout much of its range. By 2007 in Shenandoah National Park, Virginia USA, adelgids had eliminated hemlock from all permanent plots where it was present in 1991 (Anderson-Teixeira et al. 2021). Invasive insects and pathogens have also caused extensive mortality of some of the dominant tree species in swamp forests (e.g., American elm and ashes) (Barnes 1976, Abella et al. 2019). In many cases, however, the loss of these canopy dominants was compensated by increases in other tree species already present in the forests, leading to less substantial changes in ecosystem processes (e.g., carbon sequestration, litter decomposition, and water and nutrient cycling) than would be expected following persistent physiognomic change (Ellison et al. 2005).

### *4.2. Mechanisms: What are the drivers and dynamics of reorganization?*

Observations can provide valuable insights into the expression of ecosystem reorganization. However, reorganization is an emergent outcome of numerous mechanistic processes. Understanding the mechanisms that underly reorganization is key to predicting when and where such outcomes may occur (Fig. 11).

#### *4.2.1. Trigger events*

Abrupt reorganization is triggered most commonly by severe disturbance, particularly wildfire and climatic episodes that cause locally extensive mortality of dominant vegetation. Uncharacteristic disturbances can also serve as triggers, such as fire driven by the proliferation of flammable invasive species, or an unusual sequence of disturbances, e.g., severe, multi-year drought after fire, or reburns before obligate seeder species can grow old enough to produce new seeds (Coop et al. 2016, Batllori et al. 2019, Whitman et al. 2019). Large, high-severity disturbances can accelerate the pace of landscape transformation from decades to days, affecting not only overstory vegetation, but also ground cover, soils, and hydrology (Fig. 12). The energy output during extreme wildfire behavior can exceed the adaptive capacity of even fire-adapted species, overcoming their resistance to thermal stress and leading to extensive individual mortality through loss of photosynthetic apparatus, destruction of meristems, cambial and xylem damage, and damage to root systems.

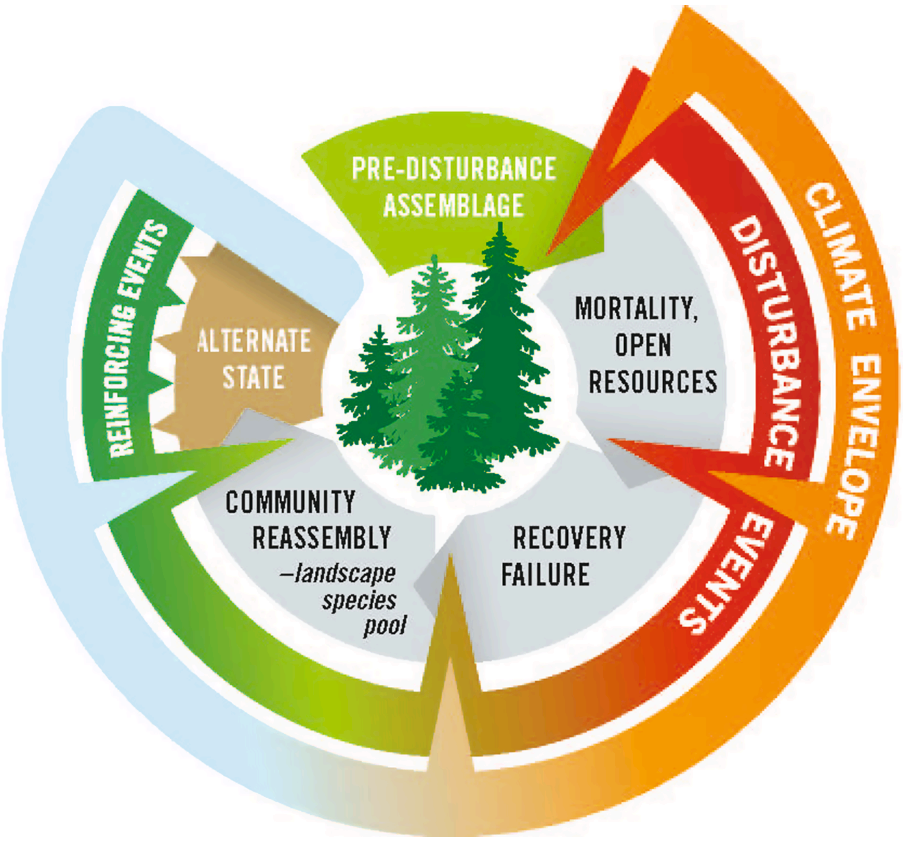


**Fig. 11.** Mechanisms of ecological reorganization. Abrupt reorganization typically follows a triggering climatic or disturbance event leading to extensive mortality. If climate and subsequent disturbance constrain recovery, community reassembly processes may result in an alternative metastable state, which is reinforced by the new climate and disturbance regime. See text for details.

Changes to the fire regime (i.e., changes in the distribution of fire intervals, severities, sizes, seasonality, etc.) can also trigger ecosystem reorganization (Hagmann et al. 2021). Van de Water and Safford (2011) and Safford and Van de Water (2014) documented fire intervals in coastal and montane ecosystems in southern California 50–100% shorter than the historical reference. Bowman et al. (2014) documented rapid population collapse of alpine ash (*Eucalyptus delegatensis* R. T. Baker), an obligate seeder, in the Australian Alps after extensive wildfires burned more than ¾ of the species range in Victoria and southeast Australia in the early 2000 s. Despite abundant post-fire seedling establishment, large portions of these fires reburned within a decade, killing nearly all of the regenerating seedlings and driving conversion to grasses and shrubs. Short-interval fires, i.e. less than the characteristic fire interval, have also been documented to overwhelm the resprouting capacity of moderate sized (22 to 36 cm diameter) fire-tolerant *Eucalyptus* (Fairman et al. 2019). Even in forest types with a high representation of serotinous species such as *Pinus contorta* var. *latifolia* (interior lodgepole pine), high frequency fire may reduce post-fire recruitment dramatically if fire return intervals are significantly shorter than mean time to first reproduction (Turner et al. 2019). Similar effects of short return intervals on recruitment have been observed in Mediterranean-climate shrublands in southwestern Australia (Enright et al. 2014) and boreal *Picea mariana* [Mill] BSP in Yukon Territory (Brown and Johnstone 2012). As climate warms and becomes increasingly conducive to widespread burning, the intervals between successive high-severity fire could become shorter; at the same time, a harsh post-fire climate could lengthen the time needed for forests to recover after severe fire, creating the “interval squeeze”, when fire re-occurs before the juvenile cohort reaches reproductive maturity (Enright et al. 2015). Modifying Baker’s (2006) equation, post-disturbance reproduction could be constrained if:

$$\frac{FRI_p}{R_a} \ll 1$$

where $FRI_p$ is the point (tree-scale) fire return interval and $R_a$ is mean time to first reproduction.

Reorganization and resulting large-scale type conversion can be triggered directly by widespread die-off driven by extended severe drought and associated hotter temperatures (Adams et al. 2009, Adams et al. 2010, Allen et al. 2010, Sankaran 2019), often covering wide geographic areas (Fettig et al. 2019, Senf et al. 2020), and sometimes triggered by extreme climate episodes such as heat waves (Lloret and Batllori 2021). Drought can cause tree mortality directly (via physiological stress, cavitation, and/or carbon starvation), or by weakening tree defenses to biotic agents such as bark beetles, defoliators, and plant pathogens (DeSoto et al. 2020); these mortality episodes can then have persistent cascading demographic effects (Law et al. 2019). Like wildfire, biotic disturbance agents are natural and essential components of forest ecosystem dynamics. However, changes in climate may affect insect and disease activity, as well as tree defenses and susceptibility (Weed et al. 2013, Anderegg et al. 2015, Hicke et al. 2016, Kautz et al. 2017). Drought and temperature stress can interact with wildfire exposure, resulting in elevated mortality rates for a given level of fire behavior (van Mantgem et al. 2018).

#### 4.2.2. *Mortality creates open resource space*

Once widespread mortality has occurred, resources (space, light, water, nutrients) become available for multiple species, not only the prior dominants. Species that are able to resprout from belowground structures after being top-killed may have an advantage in the ability to recapture growing space, both above- and below-ground (§1, *Persistence*) (Lawes and Clarke 2011, Clarke et al. 2013a) provided that fire return

**Fig. 12.** "Suspended succession" 20 years post-fire at Devil's Postpile National Monument, California, USA. Photo: Sequoia-Kings Canyon National Park Fire Effects Program, National Park Service.

intervals allow replenishment of non-structural carbohydrates used for tissue growth (Nolan et al. 2021). In a study of community assembly after a large high-severity landscape fire in southern Colorado, USA, Abella and Fornwalt (2015) found that species that either persisted or recolonized quickly constituted 62–83% of species present in the post-fire community. Similarly, 71–82% of pre-existing understory species persisted following clearcutting and broadcast burning in western Oregon, USA, whereas a smaller number of species ($n = 14$) were lost temporarily before eventually re-colonizing, and colonization by new species ($n = 11$–$19$ species/yr) occurred primarily within the first 2 years (Halpern 1988, 1989). In addition to the capacity for some species to resprout following fire-driven mortality of their above-ground parts, some species have seeds that can persist in the soil long after the adult plants that produced those seeds have been lost (Knapp et al. 2012). Persistent dormant seedbanks likely contribute to the large increases in shrub species following wildfire and prescribed burning in many mixed-conifer forests (Webster and Halpern 2010).

### *4.2.3. Recolonization failure*

Initially, pre-disturbance dominants may have an inherent advantage during the recolonization phase (Abella and Fornwalt 2015). They tend to be well adapted to local environmental conditions and typically provide local seed sources, depending on the extent and severity of disturbance. In some cases, however, population-level recovery of prior dominant species can fail or be severely limited due to soil moisture deficit and excessive evaporative demand, or disturbance-altered soil properties including the loss of soil organic matter, key limiting nutrients (Adkins et al. 2019), or essential symbionts such as mycorrhizae (Remke et al. 2020) (§3, *Recovery*). The primary mechanisms that may limit or inhibit post-fire tree seedling establishment following mortality include (1) post-disturbance landscape structure, which may limit propagule availability, especially in the case of large contiguous high-severity or treeless patches, limiting the spatial distribution of surviving mature trees and species-specific seed production and seed-dispersal capacity (Stevens et al. 2021); (2) limitations to germination, influenced by soil condition and microclimate (Chambers et al. 2016, Law et al. 2019, Burrell et al. 2021); (3) severe soil and hydrological effects following wildfire, which may prevent successful recolonization even where seed sources are available (Sidman et al. 2016, Niemeyer et al. 2020), including soil hydrophobicity, loss of soil organic matter and key limiting nutrients (Adkins et al. 2019), or essential symbionts such as mycorrhizae (Remke et al. 2020); and (4) failure of seedling establishment, driven by soil microorganisms, plant functional traits, competitive environment, and species capacity to cope with competition and climatic stress (Tercero-Bucardo et al. 2007, Enright et al. 2014, Rother and Veblen 2016, Davis et al. 2018, Simeone et al. 2019).

Flammability of the vegetation that develops after severe burning can either amplify or buffer the effects of a climate that is warming and becoming more conducive to fire (Tepley et al. 2018). Where the post-fire vegetation has low flammability, as in many boreal landscapes, resistance to reburning may limit the degree to which climate change drives increases in annual area burned, thereby extending the time available for forests to recover after severe fire (Héon et al. 2014). By contrast, where highly flammable vegetation develops after severe fire, relatively small increases in climatic potential for fire could drive extensive increases in high-severity reburns at intervals too short for forests to recover (Pausas et al. 2017). Landscapes colonized aggressively by pyrophilic and flammable shrubs after severe fire can become particularly vulnerable to extensive and persistent conversion from forest to non-forest cover (Odion et al. 2010, Kitzberger et al. 2016, Tepley et al. 2017, Batllori et al. 2019, Miller et al. 2019).

### *4.2.4. Landscape species pool*

Individual species life history and functional traits shape their responses in the post-fire environment, and ultimately drive community reorganization (Gleason 1926, Diamond 1975). Following disturbance, communities reassemble reflecting functional trait-based species responses, including intraspecific variation (Laughlin et al. 2012). Both stochastic and deterministic assembly processes guide the particular trajectory of reorganization, and new competitive hierarchies become established based on multiple species interactions that shape the new community (Temperton et al. 2004).

In the absence of significant persistence by resprouting or protected local seedbanks, community reassembly is largely dependent on species dispersing into the site, creating competitive advantages for different life history traits (e.g., dispersal ability, tolerance of poor site quality or high light levels) than those that are favored under more stable conditions (Mittelbach and Schemske 2015). Nearby undisturbed refugia and other ecological legacies can play a key role as a source of propagules into the reorganizing community (Johnstone et al. 2016). The relative increase in available space and physical resources following a large mortality event creates opportunities for species within the regional pool to establish new populations that may alter the environment for species that arrive subsequently ("priority effect") (Fukami 2015, Helsen et al. 2016).

Reorganization is dependent on the presence of species that are available to colonize and adapted to the disturbance-modified environment (Belyea and Lancaster 1999, Fukami 2015). In demographic terms, the failure of persistence and recovery of pre-disturbance dominants (Crotteau et al. 2013, Davis et al. 2020) create colonization opportunities for species better adapted to emerging climate space, e.g., drought or temperature tolerance, in the unique characteristics of post-disturbance environments (Butaye et al. 2002, Jain et al. 2012, Burrell et al. 2021). For example, Barton and Poulos (2018) found that the conversion of Madrean pine-oak forest to oak shrubland after high-severity wildfire in Arizona, USA was triggered initially by uncharacteristically high-severity fires, but oak species increased because they are better adapted to emerging conditions of drought and increasing incidence of fire. Species such as *Robinia neomexicana* (New Mexico locust), *Populus tremuloides* (aspen), *Quercus gambelii* Liebm. (Gambel oak) and shrubs in the genus *Ceanothus* are all present in pre-fire landscapes, but increase opportunistically in fire modified environments, whereas prior dominant species that depend on persistence or seed dispersal from surviving adults may experience mortality and recruitment failure (Guiterman et al. 2018).

### 4.2.5. *Community assembly processes*

During the post-disturbance period, the community re-assembles from species that either are able to persist through disturbance, or others in the landscape species pool that are able to disperse and establish successfully. Community assembly epitomizes a stochastic process: some processes, such as dispersal, are highly variable depending on dispersal mode and the landscape availability of propagules, whereas other processes (such as the environmental template or pairwise interspecific interactions) are more predictable or systematic, typically viewed as a set of successive filters (Davis et al. 2018). The net result is that community assembly is historically contingent and can be influenced strongly by priority effects, leading to niche pre-emption and niche modification by early arrivals, as well as the presence of metapopulations across the landscape (Belyea and Lancaster 1999, Fukami 2015, Mittelbach and Schemske 2015). Outcomes of community assembly processes may be better predicted by plant functional types than by species *per se* (Laughlin et al. 2012) (Figs. 10, 13).

The net result of these post-disturbance assembly processes may create multiple reorganization pathways leading to *alternative metastable states* (AMS) (Elmqvist et al. 2003, Falk 2013). Two or more community types (e.g., forest and shrubland) may co-exist in the same landscape (e.g., in a shifting mosaic that varies in response to changing disturbance frequency and patterns); alternatively, one type may become dominant under the prevailing climate and disturbance regime. Climate or an unusual disturbance event (either an uncharacteristically large or severe disturbance, or an unusual disturbance sequence) can push the landscape toward one community type, which may then persist even after the climate or disturbance regime shifts back to the conditions where both communities previously persisted. Such persistence would depend in part on stabilizing feedbacks between the community type and the climate or disturbance regime that perpetuate the existing community at the expense of the other (Miller et al. 2019). Evidence of alternative states has been demonstrated in tropical prairie-savannah-grassland mosaics in regions climatically and edaphically conducive to forest (Hoffmann et al. 2002, Staver et al. 2011, Hoffmann et al. 2012); there is increasing evidence that similar mechanisms are operating in temperate and boreal regions, or could soon operate in response to climate change (Kitzberger et al. 2016, Keyser et al. 2020, Hansen et al. 2021).

Alternative states may themselves not persist indefinitely, but there is no inherent time scale to community reorganization (Falk et al. 2019, Pausas and Bond 2020). Following type conversion, return pathways may differ from the pathway of degradation; due to altered community interactions, recovery pathways are not simply reverse travel of degradation pathways, creating the emergent property of *hysteresis* (Suding and Hobbs 2009, Litzow and Hunsicker 2016, Ratajczak et al. 2018). For example, an increase in the frequency of high-severity fire could drive extensive conversion from forest to shrubland, but a reduction in burning does not necessarily lead to a similarly abrupt return to forest cover (Tepley et al. 2018) (Fig. 13). In addition to the decades typically required for trees to grow large enough to become resistant to fire (e.g., by developing thick bark or elevated crown bases), fire-vegetation feedbacks may alter substantially the rate of return to forest cover. Where post-fire shrublands are dominated by highly flammable species, once this vegetation occupies a large portion of the landscape, much less fire may be required to maintain its dominance than was needed to initially drive the conversion from forest to shrubland. In such cases, the transition from one community type to the other may be asymmetrical: the magnitude of change in the environment or disturbance regime needed to drive the shift in one direction may be greater than that needed to drive the shift in the other direction. From an evolutionary perspective, the very fact that many species are adapted to the opportunities presented by disturbed ecosystems is a reminder that these states represent space in the evolutionary environment of species (Keeley et al. 2011b, Keeley 2012).

### 4.2.6. *Reinforcing feedbacks*

Some of the factors that initially trigger reorganization (§4.2.1) can also reinforce alternative states, effectively locking in reorganization and making it more likely to persist for extended time (Fig. 11). Here we

**Fig. 13.** Forest-shrubland conversion 28 years after the 1989 Layman Fire, Plumas NF, California, USA. *Ceanothus velutinus* dominance of former Jeffrey pine-white fir forest. Photo: DJN Young.

examine two factors that can create strong self-reinforcing feedbacks in reorganized systems.

*Disturbance*. Disturbances, such as wildfire, can be particularly effective in reinforcing an altered community state through selection for different flammability and tolerance strategies (Dantas et al. 2016, Pausas et al. 2017). In cases in which the species dominating the reorganized community are more fire-tolerant (i.e., more flammable and better able to survive or re-colonize after fire) than the pre-disturbance dominants, altered fire cycles can effectively preclude return to the prior community (Newberry et al. 2020). This dynamic is observed widely in cases of conversion from woody (tree or shrub) to grass dominance. Most grasses are highly flammable at some stage in their life cycle and have evolutionary adaptations to surviving, and even promoting, frequent fire (Gagnon et al. 2010, Pausas et al. 2017). By altering fuel types, mass, continuity, and seasonality, non-native grasses cause persistent change in the dominant fire regime type to a grass-fire cycle, creating an invasive fire regime that excludes woody plant recruitment (Brooks et al. 2004, Gaertner et al. 2014). This reinforcing feedback makes the reorganized community highly resilient in its altered state, and resistant to return to the pre-disturbance community (Brooks and Chambers 2011). Notable examples of fire-reinforced alternative states include conversion of Great Basin sage steppe to annual cheatgrass (*Bromus* Scop.) grassland (Balch et al. 2013), invasion of Sonoran upland by cool season non-native grasses (Stevens and Falk 2009, McDonald and McPherson 2011, Chambers et al. 2014), chaparral-grassland conversion in southern CA (Syphard et al. 2018, 2019) (Figure S-2), and conversions in southwestern ponderosa pine forests (Coop et al. 2020). Fire can thus play a dual role in reorganization, acting first as a trigger for initial destabilization (by causing extensive mortality and modifying the post-disturbance environment), and then as a positive feedback factor reinforcing the AMS, especially where life history adaption to fire (including flammability and the capacity to survive or re-colonize after fire) differs among species and plant functional types.

*Climate.* Like disturbance, climate can play a dual role as both a trigger and subsequent reinforcing mechanism for community reorganization (Fig. 11). Shorter (annual to multiannual) climate episodes can cause extensive mortality, creating open niche space and allowing new species to enter the community (Ruthrof et al. 2018). If the climate episode is brief, and conditions return to the normal range of variation, these effects may be transient if conditions are suitable for recovery. However, extreme climate episodes superimposed on rapidly changing mean conditions can effectively prevent prior dominants from re-establishing, even for species with long-lived individuals (Matusick et al. 2018).

Abundant evidence is accumulating of persistent species re-alignments and geographic shifts in response to changing climate (Chen et al. 2011, Iverson and McKenzie 2013, Burrows et al. 2014, Shirk et al. 2018). Altered climate conditions can favor different species once reorganization begins, if they are better adapted in terms of climate tolerance to persistent emerging conditions. For instance, field experiments evaluating seedling survival and growth under experimental warming indicate that many tree species could soon lose the capacity to regenerate in areas currently occupied by conspecific adults (Tercero-Bucardo et al. 2007, Rother et al. 2015, Hansen and Turner 2019). The degree to which these differences are projected to increase with increasing climatic warming becomes more pronounced with reduction of the buffering effect of the forest canopy, which may be expected under increasing rates of forest disturbance (Dobrowski et al. 2015, Wolf et al. 2021). Even in the absence of triggering events, changes in mean, variance, and seasonality of climate parameters can drive widespread type conversion (Williams et al. 2007, Nolan et al. 2018).

## 5. Management implications

In this synthesis, we have outlined a range of ecological resilience processes and associated mechanisms leading to persistence, recovery, and reorganization. These phases are dynamic and can occur at the scale of individuals, populations, and communities, occurring synchronously or asynchronously within and among stands. Land managers are tasked to maintain the integrity of ecosystems as dynamic entities, but there is currently no clear roadmap for how to manage these trajectories, nor what the objectives should be in a rapidly changing world. Managers are challenged to recognize the history of an area, including how it was managed by Indigenous peoples, what were its historical keystone processes, when and how these may have been interrupted, and what has transpired since then to promote or erode resilience, including logging, development, wildfire, and post-fire management. Understanding these influences on present ecosystem conditions, and how they direct a range of potential trajectories in composition and structure, is vital to devising strategies that steer ecosystem trajectories toward a desired condition (Chazdon et al. 2021). Management actions can be undertaken at any point along this sequence of resilience, and can be targeted toward a single species, groups of species (e.g., a particular plant functional group), or the community as a whole.

Forest management has long emphasized managing for persistence through restoration efforts aimed toward historical conditions (Stoddard et al. 2021). As large and severe disturbances such as droughts and fire have become more common and extensive, greater emphasis has been placed on post-disturbance recovery efforts to reverse these changes. However, in many cases recovery efforts are challenged by increasingly stressful environmental conditions and/or economic restraints and agency mandates (Guiterman et al. in preparation), or long-term changes to ecosystem function and disturbance regimes, such as mesophication of forests in eastern North America (Nowacki and Abrams 2008). Past fire management practices in many forests have distorted historical fire regimes through fire exclusion, such that fuel accumulation now makes it less likely that even fire-adapted trees will be able to regenerate and persist over large areas of high-severity fire (Keeley 2009, Stephens et al. 2018, Hagmann et al. 2021, Hagmann et al. 2022). In many areas where non-native grasses have established (Balch et al. 2013), changes can be so difficult to reverse that accepting alternative states may be the only viable pathway (Hobbs et al. 2006, Kerns et al. 2020, Lynch et al. 2021). These factors are already driving managers to consider alternative states as potential management objectives. In the sections that follow, we outline some modes of management that align with the primary resilience processes, explored further in a companion article by Guiterman et al. (in preparation) as well as other recent work (Schuurman et al. 2020, Lynch et al. 2021).

### 5.1. Managing for persistence

Managing for persistence takes advantage of the adaptation of species capacity to tolerate disturbance without major change. Persistence is often assumed to be the preferred means of maintaining ecosystem services, is usually the most socially acceptable, and may be mandated by land-management agencies (Lynch et al. 2021). Fuel treatments can reduce the risk of mortality due to fire (Stephens and Moghaddas 2005, Prichard and Kennedy 2012) and/or drought (van Mantgem et al. 2016, Restaino et al. 2019), and help post-disturbance communities to align more closely with the historical range of variation (Young et al. 2020a, Prichard et al. 2021). Stand density or basal area reduction may also assist areas adapting to the drier and warmer climate projected for coming decades (Young et al. 2020a, Tepley et al. 2020). These areas should also be able to support recurrent low- to moderate-severity fire, thus enabling persistence of keystone disturbance processes (Huffman et al. 2020). Especially at the warm/dry ecotone (Parks et al. 2019), greater moisture stress among dominant conifers (Allen and Breshears 1998, van Mantgem et al. 2009) could leave fewer large, old trees to maintain desired stand structure and composition.

Traditionally, persistence measures have focused on restoring historical conditions or dynamics (Falk 1990, Reynolds et al. 2013). Recent emphasis has included resisting changes in highly valued, culturally important areas and/or landscape refugia, and developing greater landscape heterogeneity through a mix of management practices. Refugia provide multiple benefits to sustaining biodiversity and promoting long-term recovery; often a stochastic result of heterogeneity in landform, hydrology, forest structure and composition, and recurrent fire, refugia can be created strategically ahead of disturbance through localized management actions to enhance persistence (Michalak et al. 2018, Krawchuk et al. 2020, Doxa et al. 2022). Another important strategy to generate a diverse mosaic across many landscapes is to reinstate or emulate indigenous fire use (Kimmerer and Lake 2001). Small-scale, frequent burning that was common historically among many indigenous communities in North America (and has been returned to some areas) limits the intensity and spread of wildfires through fuel reduction, aiding in the persistence of overstory structure and composition (Lake et al. 2017, Roos et al. 2021). Managing at large spatial scales, taking advantage of resilience mechanisms among species and communities, integrating indigenous styles of management through collaborations with knowledge-keepers, and utilizing the refugia of past disturbances can help to promote persistence in the face of extreme events and changing baseline climate conditions (Stevens et al. 2021).

### 5.2. *Managing for recovery*

As more forested area is affected by large and severe disturbance, management is turning increasingly toward recovery efforts to recoup potential losses to resources and values. Optimizing recovery following major disturbance draws on the deep knowledge of land managers to initiate and facilitate recruitment and colonization of desired pre-disturbance dominant species through various species- and site-level strategies. Natural regeneration of seed-obligate species can occur relatively quickly on some sites when conditions are favorable (Figs. 5, 6, S-1) (Harvey et al. 2016, Tepley et al. 2017, Urza and Sibold 2017). Forest managers can often anticipate the trajectory of a stand based on initial post-disturbance vegetation. For example, initial dominance of shrubs with little tree regeneration may indicate that a site may remain shrub-dominated for decades or longer (Airey Lauvaux et al. 2016, Guiterman et al. 2018). One of the primary indicators of likely recovery failure following disturbance is the absence of a nearby seed source for the previously dominant species (§4.3 *Recolonization failure*). New tools allow managers to predict conifer re-establishment (or lack thereof) following fire (Stewart et al. 2021, Tubbesing et al. 2021), and the success of post-fire tree planting relative to natural tree establishment based on residual tree seed source maps and other environmental variables.

The spatial scale of the recovery site is critical, because smaller sites may have adequate parent trees nearby (within ~ 60–100 m), alleviating the need for planting (Ouzts et al. 2015, Owen et al. 2017, Stevens-Rumann and Morgan 2019). Site conditions following high-severity fire, in particular, can be challenging for regeneration (Feddema et al. 2013), especially in large patches ($10^3$–$10^4$ ha) or following salvage operations (Lindenmayer et al. 2012). Analysis of the spatial arrangement of refugia as a seed source and other environmental conditions can highlight areas that may require planting in order for pre-disturbance species to recover rapidly (Stevens-Rumann and Morgan 2019, Stevens et al. 2021, Stewart et al. 2021). North et al. (2019) introduced a zonal framework for post-disturbance reforestation efforts that includes utilizing selective planting locations to establish “founder stands.” This may be effective because it (i) capitalizes on advantageous conditions for seedlings from variability in soil moisture and topography (Rother and Veblen 2016), and (ii) does not require the extensive resources needed for continuous planting of a large area. Residual or newly accumulated fuel loads following high-severity fire or other disturbances may be high, which can both facilitate regeneration by providing moisture retention while also posing a threat to recovery if the site should burn again (Keyser et al. 2020). Seeds for focal reforestation species can be obtained from non-local ecotypes believed to be better adapted to the new conditions at the planting site (Aitken and Bemmels, 2016; Young et al., 2020b).

### 5.3. *Managing reorganization*

The capacity of a system to reorganize is an expression of ecological resilience in the face of changing conditions. In some cases, reorganization may benefit both the ecosystem and society. For example, pushing a site toward a non-forest state could be an act of restoration, as in the case of montane meadows encroached upon by conifers (Matonis and Binkley 2018). However, in other cases sites may reorganize into less desirable conditions, such as shrublands in formerly forested areas, which could persist for centuries (Guiterman et al. 2018). At broader spatial scales, diverse landscape mosaics appear to have been characteristic of resilient ecosystems under historical conditions, creating a complex balance among the forces of soils, climate, and disturbance (Hessburg et al. 1999, Cansler et al. 2018). In recent years, uncharacteristically large and/or severe wildfire events have affected landscape forest structure, triggering transitions across large areas; it remains unclear whether these events will enhance landscape diversity and resilience, or erode it. Anticipating major transitions could help increase chances of success, enhance the resilience of refugia areas, and protect ecosystem services (Millar and Stephenson 2015). Promoting a diverse landscape-scale mosaic of forest, shrubland, and grassland ahead of major disturbance events including wildfire can moderate changes associated with widespread vegetation type conversion (Lynch et al. 2021, Stevens et al. 2021).

In many areas of western North America, extensive transitions are already underway, including chaparral, sagebrush, and desert systems converting to non-native grasses, and many forests converting to shrublands (Guiterman et al. in preparation). Type conversions are now a common consequence of anthropogenic stressors on ecological communities (Stevens-Rumann et al. 2018, Batllori et al. 2020, Coop et al. 2020). Managing these areas is challenging due to the frequency and spatial scale of change, with limited funding or social support to attempt large-scale recovery. Moreover, managers can be overwhelmed by uncertainties regarding the trajectory of natural recovery, efficacy of recovery efforts (many of which may fail or are experimental), or whether there is social license to introduce species that could be more tolerant of emerging conditions. In many areas, these hurdles have slowed or stalled management actions in type-converted areas, with the result that active management may occur on only a relatively small fraction of affected areas (Guiterman et al. in preparation). In cases where persistence and recovery are unlikely and reorganization is inevitable, managers could view this as an opportunity to direct reorganization toward a more desirable future state, instead of as a strictly negative outcome.

Given the frequency and scale of type conversions across western North America, further research is needed to resolve uncertainties by documenting successes and failures. Experiments and trials present key opportunities for co-production between scientists and managers (Krawchuk et al. 2020), and avenues to apply indigenous knowledge of long-term ecosystem resilience. Resilience frameworks described here and elsewhere (Schuurman et al. 2020, Lynch et al. 2021) can offer crucial guidelines for planning and decision making in an era of widespread and rapid ecological change.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgments

The authors thank David Breshears, Steve Ostoja, and two anonymous reviewers for their valuable comments and suggestions. Figs. 1 and 11 were prepared by Regole Design Inc (Tucson, AZ USA). This project was supported by the U.S. Geological Survey's Southwest Climate Adaptation Science Center (G19AC00099) and Ecosystems Mission Area. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120129.

## References

Abatzoglou, J.T., Kolden, C.A., 2013. Relationships between climate and macroscale area burned in the western United States. Int. J. Wildland Fire 22, 1003–1020.

Abella, S.R., 2009. Smoke-cued emergence in plant species of ponderosa pine forests: contrasting greenhouse and field results. Fire Ecol. 5, 22–37.

Abella, S.R., Fornwalt, P.J., 2015. Ten years of vegetation assembly after a North American mega fire. Glob. Change Biol. 21, 789–802.

Abella, S.R., Hausman, C.E., Jaeger, J.F., Menard, K.S., Schetter, T.A., Rocha, O.J., 2019. Fourteen years of swamp forest change from the onset, during, and after invasion of emerald ash borer. Biol. Invasions 21, 3685–3696.

Adams, H.D., Guardiola-Claramonte, M., Barron-Gafford, G.A., Villegas, J.C., Breshears, D.D., Zou, C.B., Troch, P.A., Huxman, T.E., 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. Proc. Natl. Acad. Sci. 106, 7063–7066.

Adams, H.D., Macalady, A.K., Breshears, D.D., Allen, C.D., Stephenson, N.L., Saleska, S. R., Huxman, T.E., McDowell, N.G., 2010. Climate-induced tree mortality: Earth system consequences. Eos, Trans. Am. Geophys. Union 91, 153–154.

Adams, H.D., Zeppel, M.J.B., Anderegg, W.R.L., Hartmann, H., Landhäusser, S.M., Tissue, D.T., Huxman, T.E., Hudson, P.J., McDowell, N.G., et al., 2017. A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. Nat. Ecol. Evol. 1, 1285–1291.

Adkins, J., Sanderman, J., Miesel, J., 2019. Soil carbon pools and fluxes vary across a burn severity gradient three years after wildfire in Sierra Nevada mixed-conifer forest. Geoderma 333, 10–22.

Airey Lauvaux, C., Skinner, C.N., Taylor, A.H., 2016. High severity fire and mixed conifer forest-chaparral dynamics in the southern Cascade Range, USA. For. Ecol. Manage. 363, 74–85.

Aitken, S.N., Bemmels, J.B., 2016. Time to get moving: assisted gene flow of forest trees. Evol. Appl. 9, 271–290.

Allen, C.D., Breshears, D.D., 1998. Drought-induced shift of a forest/woodland ecotone: Rapid landscape response to climate variation. Proc. Natl. Acad. Sci. 95, 14839–14842.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Casto, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. 259, 660–684.

Allen, R., 1987. Ecology of Nothofagus menziesii in the catlins ecological region, South-east Otago, New Zealand (I) seed production, viability, and dispersal. N. Z. J. Botan. 25, 5–10.

Andela, N., Morton, D., Giglio, L., Chen, Y., Van Der Werf, G., Kasibhatla, P., DeFries, R., Collatz, G., Hantson, S., Kloster, S., 2017. A human-driven decline in global burned area. Science 356, 1356–1362.

Anderegg, W.R., Berry, J.A., Smith, D.D., Sperry, J.S., Anderegg, L.D., Field, C.B., 2012. The roles of hydraulic and carbon stress in a widespread climate-induced forest die-off. Proc. Natl. Acad. Sci. 109, 233–237.

Anderegg, W.R., Hicke, J.A., Fisher, R.A., Allen, C.D., Aukema, J., Bentz, B., Hood, S., Lichstein, J.W., Macalady, A.K., McDowell, N., 2015. Tree mortality from drought, insects, and their interactions in a changing climate. New Phytol. 208, 674–683.

Anderson-Teixeira, K.J., Herrmann, V., Cass, W.B., Williams, A.B., Paull, S.J., Gonzalez-Akre, E.B., Helcoski, R., Tepley, A.J., Bourg, N.A., Cosma, C.T., 2021. Long-Term Impacts of Invasive Insects and Pathogens on Composition, Biomass, and Diversity of Forests in Virginia's Blue Ridge Mountains. Ecosystems 24, 89–105.

Arizpe, A.H., 2016. Widespread Fire Years in Conifer Forests are Contingent on Both Winter and Monsoon Precipitation in the US-Mexico Sky Islands. University of Arizona, Tucson, AZ. MS Thesis.

Armenteras, D., Dávalos, L.M., Barreto, J.S., Miranda, A., Hernández-Moreno, A., Zamorano-Elgueta, C., González-Delgado, T.M., Meza-Elizalde, M.C., Retana, J., 2021. Fire-induced loss of the world's most biodiverse forests in Latin America. Sci. Adv. 7 (eabd3357).

Baker, W.L., 2006. Fire and restoration of sagebrush ecosystems. Wildl. Soc. Bull. 34, 177–185.

Balch, J.K., Bradley, B.A., D'Antonio, C.M., Gómez-Dans, J., 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). Glob. Change Biol. 19, 173–183.

Barnes, B.V., 1976. Succession in deciduous swamp communities of southeastern Michigan formerly dominated by American elm. Can. J. Bot. 54, 19–24.

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., 2011. Has the Earth's sixth mass extinction already arrived? Nature 471, 51–57.

Barton, A.M., Poulos, H.M.J.F.e., 2018. Pine vs. oaks revisited: Conversion of Madrean pine-oak forest to oak shrubland after high-severity wildfire in the Sky Islands of Arizona. For. Ecol. Manage. 414, 28–40.

Batllori, E., De Cáceres, M., Brotons, L., Ackerly, D.D., Moritz, M.A., Lloret, F., 2019. Compound fire-drought regimes promote ecosystem transitions in Mediterranean ecosystems. J. Ecol. 107, 1187–1198.

Batllori, E., Lloret, F., Aakala, T., Anderegg, W.R., Aynekulu, E., et al., 2020. Forest and woodland replacement patterns following drought-related mortality. Proc. Natl. Acad. Sci. 117, 29720–29729.

Batllori, E., Parisien, M.A., Krawchuk, M.A., Moritz, M.A., 2013. Climate change-induced shifts in fire for Mediterranean ecosystems. Glob. Ecol. Biogeogr. 22, 1118–1129.

Bauer, G., Speck, T., Blömer, J., Bertling, J., Speck, O., 2010. Insulation capability of the bark of trees with different fire adaptation. J. Mater. Sci. 45, 5950–5959.

Beisner, B., Haydon, D., Cuddington, K., 2003. Alternative stable states in ecology. Front. Ecol. Environ. 1, 376–382.

Belyea, L.R., Lancaster, J., 1999. Assembly rules within a contingent ecology. Oikos 86, 402–416.

Bennett, A.C., McDowell, N.G., Allen, C.D., Anderson-Teixeira, K.J., 2015. Larger trees suffer most during drought in forests worldwide. Nat. Plants 1, 15139.

Bentz, B.J., Régnière, J., Fettig, C.J., Hansen, E.M., Hayes, J.L., Hicke, J.A., Kelsey, R.G., Negrón, J.F., Seybold, S.J., 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. Bioscience 60, 602–613.

Binkley, D., 2021. Forest Ecology: An Evidence-based Approach. NJ, USA, Wiley-Blackwell, Hoboken.

Bond, W.J., 2019. Open ecosystems: ecology and evolution beyond the forest edge. Oxford University Press.

Bond, W.J., Van Wilgen, B.W., 2012. Fire and plants. Springer Science & Business Media.

Bonnet, V.H., Schoettle, A.W., Shepperd, W.D., 2005. Postfire environmental conditions influence the spatial pattern of regeneration for Pinus ponderosa. Can. J. For. Res. – Revue Canadienne De Recherche Forestiere 35, 37–47.

Bowman, D.M., Murphy, B.P., Neyland, D.L., Williamson, G.J., Prior, L.D., 2014. Abrupt fire regime change may cause landscape-wide loss of mature obligate seeder forests. Glob. Change Biol. 20, 1008–1015.

Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W. H., Kastens, J.H., Floyd, M.L., Belnap, J., 2005. Regional vegetation die-off in response to global-change-type drought. Proc. Natl. Acad. Sci. 102, 15144–15148.

Brito-Morales, I., Molinos, J.G., Schoeman, D.S., Burrows, M.T., Poloczanska, E.S., Brown, C.J., Ferrier, S., Harwood, T.D., Klein, C.J., McDonald-Madden, E., 2018. Climate velocity can inform conservation in a warming world. Trends Ecol. Evol. 33, 441–457.

Brooks, M.L., Chambers, J.C., 2011. Resistance to invasion and resilience to fire in desert shrublands of North America. Rangeland Ecol. Manage. 64, 431–438.

Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., DiTomaso, J. M., Hobbs, R.J., Pellant, M., Pyke, D., 2004. Effects of invasive alien plants on fire regimes. Bioscience 54, 677–688.

Brown, C.D., Johnstone, J.F., 2012. Once burned, twice shy: Repeat fires reduce seed availability and alter substrate constraints on Picea mariana regeneration. For. Ecol. Manage. 266, 34–41.

Burns, R.M., Honkala, B.H., 1990. Silvics of North America, Volume 1. Conifers, USDA Forest Service (Washington).

Burrell, A., Kukavskaya, E., Baxter, R., Sun, Q., Barrett, K., 2021. Post-fire recruitment failure as a driver of forest to non-forest ecosystem shifts in boreal regions. In: Ecosystem Collapse and Climate Change. Springer, pp. 69–100.

Burrows, M.T., Schoeman, D.S., Richardson, A.J., Molinos, J.G., Hoffmann, A., Buckley, L.B., Moore, P.J., Brown, C.J., Bruno, J.F., Duarte, C.M., 2014. Geographical limits to species-range shifts are suggested by climate velocity. Nature 507, 492.

Butaye, J., Jacquemyn, H., Honnay, O., Hermy, M., 2002. The species pool concept applied to forests in a fragmented landscape: dispersal limitation versus habitat limitation. J. Veg. Sci. 13, 27–34.

Cansler, C.A., McKenzie, D., Halpern, C.B., 2018. Fire enhances the complexity of forest structure in alpine treeline ecotones. Ecosphere 9, e02091.

Chambers, J.C., Bradley, B.A., Brown, C.S., D'Antonio, C., Germino, M.J., Grace, J.B., Hardegree, S.P., Miller, R.F., Pyke, D.A., 2014. Resilience to Stress and Disturbance, and Resistance to Bromus tectorum L. Invasion in Cold Desert Shrublands of Western North America. Ecosystems 17, 360–375.

Chambers, M.E., Fornwalt, P.J., Malone, S.L., Battaglia, M.A., 2016. Patterns of conifer regeneration following high severity wildfire in ponderosa pine – dominated forests of the Colorado Front Range. For. Ecol. Manage. 378, 57–67.

Chase, J.M., 2003. Community assembly: when should history matter? Oecologia 136, 489–498.

Chazdon, R.L., Falk, D.A., Banin, L.F., Wagner, M., Wilson, S., Grabowski, R.C., Suding, K.N., 2021. The intervention continuum in restoration ecology: rethinking the active-passive dichotomy. Restor. Ecol.

Chen, I.C., Hill, J.K., Ohlemüller, R., Roy, D.B., Thomas, C.D., 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333, 1024–1026.

Choat, B., Brodribb, T.J., Brodersen, C.R., Duursma, R.A., Lopez, R., Medlyn, B.E., 2018. Triggers of tree mortality under drought. Nature 558, 531–539.

Clark, J.S., 1998. Why trees migrate so fast: Confronting theory with dispersal biology and the paleorecord. Am. Nat. 152, 204–224.

Clark, J.S., Beckage, B., Camill, P., Cleveland, B., HilleRisLambers, J., Lichter, J., McLachlan, J., Mohan, J., Wyckoff, P., 1999. Interpreting recruitment limitation in forests. Am. J. Bot. 86, 1–16.

Clark, J.S., Lynch, J., Stocks, B.J., Goldammer, J.G., 1998. Relationships between charcoal particles in air and sediments in west-central Siberia. Holocene 8, 19–29.

Clarke, P.J., Lawes, M., Midgley, J.J., Lamont, B., Ojeda, F., Burrows, G., Enright, N., Knox, K., 2013. Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. New Phytol. 197, 19–35.

Clarke, P.J., Lawes, M.J., Murphy, B.P., Russell-Smith, J., Nano, C.E., Bradstock, R., Enright, N.J., Fontaine, J.B., Gosper, C.R., Radford, I., 2015. A synthesis of postfire recovery traits of woody plants in Australian ecosystems. Sci. Total Environ. 534, 31–42.

Clements, F.E., 1936. Nature and structure of the climax. J. Ecol. 24, 252–284.

Collins, B.M., Miller, J.D., Knapp, E.E., Sapsis, D.B., 2019. A quantitative comparison of forest fires in central and northern California under early (1911–1924) and contemporary (2002–2015) fire suppression. Int. J. Wildland Fire 28, 138–148.

Collins, L., 2020. Eucalypt forests dominated by epicormic resprouters are resilient to repeated canopy fires. J. Ecol. 108, 310–324.

Colwell, R.K., Rangel, T.F., 2009. Hutchinson's duality: The once and future niche. Proc. Natl. Acad. Sci. 106, 19651–19658.

Comte, L., Murienne, J., Grenouillet, G., 2014. Species traits and phylogenetic conservatism of climate-induced range shifts in stream fishes. Nat. Commun. 5, 1–9.

Coop, J.D., Givnish, T.J., 2007. Spatial and temporal patterns of recent forest encroachment in montane grasslands of the Valles Caldera, New Mexico, USA: Valles Caldera tree-line shift. J. Biogeogr. 34, 914–927.

Coop, J.D., Parks, S.A., McClernan, S.R., Holsinger, L.M., 2016. Influences of prior wildfires on vegetation response to subsequent fire in a reburned southwestern landscape. Ecol. Appl. 26, 346–354.

Coop, J.D., DeLory, T.J., Downing, W.M., Haire, S.L., Krawchuk, M.A., Miller, C., Parisien, M.A., Walker, R.B., 2019. Contributions of fire refugia to resilient ponderosa pine and dry mixed-conifer forest landscapes. Ecosphere 10, e02809.

Coop, J.D., Parks, S.A., Stevens-Rumann, C.S., Crausbay, S.D., Higuera, P.E., Hurteau, M. D., Tepley, A., Whitman, E., Assal, T., Collins, B.M., Davis, K.T., Dobrowski, S.Z., Falk, D.A., Fornwalt, P.J., Fule, P.Z., Harvey, B.J., Kane, V.R., Littlefield, C.E., Margolis, E.Q., North, M., Parisien, M.-A., Prichard, S., Rodmen, K.C., 2020. Wildfire-driven forest conversion in western North American landscapes. Bioscience 70, 659–673.

Crausbay, S.D., Higuera, P.E., Sprugel, D.G., Brubaker, L.B., 2017. Fire catalyzed rapid ecological change in lowland coniferous forests of the Pacific Northwest over the past 14,000 years. Ecology 98, 2356–2369.

Crotteau, J.S., Varner III, J.M., Ritchie, M.W., 2013. Post-fire regeneration across a fire severity gradient in the southern Cascades. For. Ecol. Manage. 287, 103–112.

Curtis, P.G., Slay, C.M., Harris, N.L., Tyukavina, A., Hansen, M.C., 2018. Classifying drivers of global forest loss. Science 361, 1108–1111.

Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, A.E., Peterson, C.J., Simberloff, D., Swanson, F.J., Stocks, B.J., Wotton, B.M., 2001. Climate change and forest disturbances. Bioscience 51, 723–734.

Dantas, V.d.L., Hirota, M., Oliveira, R.S., Pausas, J.G., 2016. Disturbance maintains alternative biome states. Ecol. Lett. 19, 12–19.

Davis, K.T., Dobrowski, S.Z., Higuera, P.E., Holden, Z.A., Veblen, T.T., Rother, M.T., Parks, S.A., Sala, A., Maneta, M.P., 2019. Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. Proc. Natl. Acad. Sci. 116, 6193–6198.

Davis, K.T., Higuera, P.E., Dobrowski, S.Z., Parks, S.A., Abatzoglou, J.T., Rother, M.T., Veblen, T.T., 2020. Fire-catalyzed vegetation shifts in ponderosa pine and Douglas-fir forests of the western United States. Environ. Res. Lett. 15:1040b1048.

Davis, K.T., Higuera, P.E., Sala, A., 2018. Anticipating fire-mediated impacts of climate change using a demographic framework. Funct. Ecol. 32, 1729–1745.

Davis, M.B., Shaw, R.G., Etterson, J.R., 2005. Evolutionary responses to changing climate. Ecology 86, 1704–1714.

Davis, S.D., Ewers, F.W., Sperry, J.S., Portwood, K.A., Crocker, M.C., Adams, G.C., 2002. Shoot dieback during prolonged drought in Ceanothus (Rhamnaceae) chaparral of California: a possible case of hydraulic failure. Am. J. Bot. 89, 820–828.

DeSoto, L., Cailleret, M., Sterck, F., Jansen, S., Kramer, K., Robert, E.M.R., Aakala, T., Amoroso, M.M., Bigler, C., Camarero, J.J., Čufar, K., Gea-Izquierdo, G., Gillner, S., Haavik, L.J., Hereş, A.-M., Kane, J.M., Kharuk, V.I., Kitzberger, T., Klein, T., Levanič, T., Linares, J.C., Mäkinen, H., Oberhuber, W., Papadopoulos, A., Rohner, B., Sangüesa-Barreda, G., Stojanovic, D.B., Suárez, M.L., Villalba, R., Martínez-Vilalta, J., 2020. Low growth resilience to drought is related to future mortality risk in trees. Nat. Commun. 11, 545.

Diamond, J.M., 1975. Assembly of species communities. In: Cody, M.L., Diamond, J.M. (Eds.), Ecology & evolution of communities. Belknap Press, Cambridge, MA, pp. 342–444.

Dobrowski, S.Z., Swanson, A.K., Abatzoglou, J.T., Holden, Z.A., Safford, H.D., Schwartz, M.K., Gavin, D.G., 2015. Forest structure and species traits mediate projected recruitment declines in western US tree species. Glob. Ecol. Biogeogr. 24, 917–927.

Dolanc, C.R., Safford, H.D., Dobrowski, S.Z., Thorne, J.H., 2014. Twentieth century shifts in abundance and composition of vegetation types of the S ierra N evada, CA, US. Appl. Veg. Sci. 17, 442–455.

Donato, D.C., Fontaine, J.B., Campbell, J.L., Robinson, W.D., Kauffman, J.B., Law, B.E., 2009. Conifer regeneration in stand-replacement portions of a large mixed-severity wildfire in the Klamath-Siskiyou Mountains. Can. J. For. Res. 39, 823–838.

Doxa, A., Kamarianakis, Y., Mazaris, A.D., 2022. Spatial heterogeneity and temporal stability characterize future climatic refugia in Mediterranean Europe. Global Change Biol. 1–12 https://doi.org/10.1111/gcb.16072.

Earles, J.M., North, M.P., Hurteau, M.D., 2014. Wildfire and drought dynamics destabilize carbon stores of fire-suppressed forests. Ecol. Appl. 24, 732–740.

Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Front. Ecol. Environ. 3, 479–486.

Eidenshink, J.C., Schwind, B., Brewer, K., Zhu, Z.-L., Quayle, B., Howard, S.M., 2007. A project for monitoring trends in burn severity. Fire Ecol. 3, 3–21.

Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., Norberg, J., 2003. Response diversity, ecosystem change, and resilience. Front. Ecol. Environ. 1, 488–494.

Engber, E.A., Varner, J.M., Arguello, L.A., Sugihara, N.G., 2011. The Effects of Conifer Encroachment and Overstory Structure on Fuels and Fire in an Oak Woodland Landscape. Fire Ecol. 7, 32–50.

Enright, N.J., Fontaine, J.B., Bowman, D.M., Bradstock, R.A., Williams, R.J., 2015. Interval squeeze: altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. Front. Ecol. Environ. 13, 265–272.

Enright, N.J., Fontaine, J.B., Lamont, B.B., Miller, B.P., Westcott, V.C., 2014. Resistance and resilience to changing climate and fire regime depend on plant functional traits. J. Ecol. 102, 1572–1581.

Erikkson, O., 1996. Regional dynamics of plants: a review of evidence for remnant, source-sink, and metapopulations. Oikos 77, 248–258.

Fairman, T.A., Bennett, L.T., Nitschke, C.R., 2019. Short-interval wildfires increase likelihood of resprouting failure in fire-tolerant trees. J. Environ. Manage. 231, 59–65.

Falk, D.A., 1990. Discovering the past, creating the future. Restoration Manage. Notes 8, 71–72.

Falk, D.A., 2013. Are Madrean ecosystems approaching tipping points? Anticipating interactions of landscape disturbance and climate change.*in* Merging science and management in a rapidly changing world: Biodiversity and management of the Madrean Archipelago III. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. Fort Collins, CO., Tucson, AZ.

Falk, D.A., 2017. Restoration Ecology, Resilience, and the Axes of Change. Ann. Mo. Bot. Gard. 102, 201–217.

Falk, D.A., Watts, A.C., Thode, A.E., 2019. Scaling ecological resilience. Front. Ecol. Evol. 7, 275.

Feddema, J.J., Mast, J.N., Savage, M., 2013. Modeling high-severity fire, drought and climate change impacts on ponderosa pine regeneration. Ecol. Model. 253, 56–69.

Fernandez, M.C., Hu, F.S., Gavin, D.G., de Lafontaine, G., Heath, K.D., 2021. A tale of two conifers: Migration across a dispersal barrier outpaced regional expansion from refugia. J. Biogeogr. 48, 2133–2143.

Fettig, C.J., Mortenson, L.A., Bulaon, B.M., Foulk, P.B., 2019. Tree mortality following drought in the central and southern Sierra Nevada, California, U.S. For. Ecol. Manage. 432, 164–178.

Fletcher, M.-S., Wood, S.W., Haberle, S.G., 2014. A fire-driven shift from forest to non-forest: evidence for alternative stable states? Ecology 95, 2504–2513.

Fukami, T., 2015. Historical contingency in community assembly: integrating niches, species pools, and priority effects. Annu. Rev. Ecol. Evol. Syst. 46, 1–23.

Furniss, T.J., Das, A.J., van Mantgem, P.J., Stephenson, N.L., Lutz, J.A., 2022. Croswding, climate, and the case for social distancing among trees. Ecol. Appl.

Furniss, T.J., Larson, A.J., Kane, V.R., Lutz, J.A., 2019. Multi-scale assessment of post-fire tree mortality models. Int. J. Wildland Fire 28, 46.

Gaertner, M., Biggs, R., Te Beest, M., Hui, C., Molofsky, J., Richardson, D.M., 2014. Invasive plants as drivers of regime shifts: identifying high-priority invaders that alter feedback relationships. Divers. Distrib. 20, 733–744.

Gagnon, P.R., Passmore, H.A., Platt, W.J., Myers, J.A., Paine, C.T., Harms, K.E., 2010. Does pyrogenicity protect burning plants? Ecology 91, 3481–3486.

Gedalof, Z., Peterson, D.L., Mantua, N., 2005. Atmospheric, climatic, and ecological controls on extreme wildfire. Ecol. Appl. 15, 154–174.

Gleason, H.A., 1926. The individualistic concept of the plant association. Bull. Torrey Bot. Club 53, 7–26.

Gray, A.N., Spies, T.A., 1997. Microsite controls on tree seedling establishment in conifer forest canopy gaps. Ecology 78, 2458–2473.

Greene, D.F., Canham, C.D., Coates, K.D., Lepage, P.T., 2004. An evaluation of alternative dispersal functions for trees. J. Ecol. 92, 758–766.

Greene, D.F., Johnson, E.A., 1996. Wind Dispersal of Seeds from a Forest Into a Clearing. Ecology 77, 595–609.

Greene, D.F., Zasada, J.C., Sirois, L., Kneeshaw, D., Morin, H., Charron, I., Simard, M.-J., 1999. A review of the regeneration dynamics of North American boreal forest tree species. Can. J. For. Res. 29, 824–839.

Grubb, P.J., 1977. The maintenance of species-richness in plant communities: The importance of the regeneration niche. Biol. Rev. 52, 107–145.

Guiterman, C.H., Gregg, R.M., Marshall, L.A.E., Beckmann, J.J., van Mantgem, P., Falk, D.A., Keeley, J.E., et al. in preparation. Vegetation type conversion in the US Southwest: Drivers, management responses, future directions. Fire Ecol.

Guiterman, C.H., Margolis, E.Q., Allen, C.D., Falk, D.A., Swetnam, T.W., 2018. Long-Term Persistence and Fire Resilience of Oak Shrubfields in Dry Conifer Forests of Northern New Mexico. Ecosystems 21, 943–959.

Hagmann, R., Hessburg, P., Prichard, S., Povak, N., Brown, P., Fulé, P., Keane, R., Knapp, E., Lydersen, J., Metlen, K., Reilly, M., Meador, A.S., Stephens, S., Stevens, J., Taylor, A., Yocom, L., Battaglia, M., Churchill, D., Daniels, L., Falk, D., Krawchuk, M., Johnston, J., Levine, C., Meigs, G., Merschel, A., North, M., Safford, H., Swetnam, T., Waltz, A., 2021. Evidence for widespread changes in the structure, composition, and fire regimes of western North American forests. Ecol. Appl. 31, e02431.

Hagmann, R., Hessburg, P., Salter, R., Merschel, A., Reilly, M., 2022. Contemporary wildfires further degrade resistance and resilience of fire-excluded forests. For. Ecol. Manage. 506, 119975.

Haire, S.L., McGarigal, K., 2010. Effects of landscape patterns of fire severity on regenerating ponderosa pine forests (Pinus ponderosa) in New Mexico and Arizona, USA. Landscape Ecol. 25, 1055–1069.

Halofsky, J.E., Peterson, D.L., Harvey, B.J., 2020. Changing wildfire, changing forests: the effects of climate change on fire regimes and vegetation in the Pacific Northwest, USA. Fire Ecol. 16, 4.

Halpern, C.B., 1988. Early successional pathways and the resistance and resilience of forest communities. Ecology 69, 1703–1715.

Halpern, C.B., 1989. Early successional patterns of forest species: Interactions of life history traits and disturbance. Ecology 70, 704–720.

Halpern, C.B., Antos, J.A., 2021. Rates, patterns, and drivers of tree reinvasion 15 years after large-scale meadow-restoration treatments. Restoration. Ecology:e13377.

Halpern, C.B., Antos, J.A., Rice, J.M., Haugo, R.D., Lang, N.L., 2010. Tree invasion of a montane meadow complex: temporal trends, spatial patterns, and biotic interactions. J. Veg. Sci. 21, 717–732.

Hammond, W.M., Yu, K., Wilson, L.A., Will, R.E., Anderegg, W.R., Adams, H.D., 2019. Dead or dying? Quantifying the point of no return from hydraulic failure in drought-induced tree mortality. New Phytol. 223, 1834–1843.

Hannah, L., Flint, L., Syphard, A.D., Moritz, M.A., Buckley, L.B., McCullough, I.M., 2014. Fine-grain modeling of species' response to climate change: holdouts, stepping-stones, and microrefugia. Trends Ecol. Evol. 29, 390–397.

Hansen, W.D., Braziunas, K.H., Rammer, W., Seidl, R., Turner, M.G., 2018. It takes a few to tango: changing climate and fire regimes can cause regeneration failure of two subalpine conifers. Ecology 99, 966–977.

Hansen, W.D., Fitzsimmons, R., Olnes, J., Williams, A.P., 2021. An alternate vegetation type proves resilient and persists for decades following forest conversion in the North American boreal biome. J. Ecol. 109, 85–98.

Hansen, W.D., Turner, M.G., 2019. Origins of abrupt change? Postfire subalpine conifer regeneration declines nonlinearly with warming and drying. Ecol. Monogr. 89, e01340.

Harper, J.L., 1977. Population biology of plants. Academic Press, London, UK.

Harvey, B.J., Donato, D.C., Turner, M.G., 2016. High and dry: post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches. Glob. Ecol. Biogeogr. 25, 655–669.

Helsen, K., Hermy, M., Honnay, O., 2016. A test of priority effect persistence in semi-natural grasslands through the removal of plant functional groups during community assembly. BMC Ecol. 16, 22.

Héon, J., Arseneault, D., Parisien, M.-A., 2014. Resistance of the boreal forest to high burn rates. Proc. Natl. Acad. Sci. 111, 13888–13893.

Hessburg, P.F., Smith, B.G., Kreiter, S.G., 1999. Historical and current forest and range landscapes in the Interior Columbia River basin including portions of the Klamath and Great Basins. Part I: Linking vegetation patterns and landscape vulnerability to potential insect and pathogen disturbances. General Technical Report General Technical Report PNW-GTR-458, USDA Forest Service, Pacific Northwest Research Station, Portland, OR.

Hicke, J.A., Meddens, A.J., Kolden, C.A., 2016. Recent tree mortality in the western United States from bark beetles and forest fires. For. Sci. 62, 141–153.

Higgs, E., Falk, D.A., Guerrini, A., Hall, M., Harris, J., Hobbs, R.J., Jackson, S.T., Rhemtulla, J.M., Throop, W., 2014. The changing role of history in restoration ecology. Front. Ecol. Environ. 12, 499–506.

Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A., Epstein, P. R., Ewel, J.J., Klink, C.A., Lugo, A.E., Norton, D., Ojima, D., Richardson, D.M., Sanderson, E.W., Valladares, F., Vilà, M., Zamora, R., Zobel, M., 2006. Novel ecosystems: Theoretical and management aspects of the new ecological world order. Glob. Ecol. Biogeogr. 15, 1–7.

Hoffmann, W.A., Geiger, E.L., Gotsch, S.G., Rossatto, D.R., Silva, L.C., Lau, O.L., Haridasan, M., Franco, A.C., 2012. Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. Ecol. Lett. 15, 759–768.

Hoffmann, W.A., Orthen, B., Do Nascimento, P.K.V., 2003. Comparative fire ecology of tropical savanna and forest trees. Functional Ecology:720–726.

Hoffmann, W.A., Schroeder, W., Jackson, R.B., 2002. Positive feedbacks of fire, climate, and vegetation and the conversion of tropical savanna. Geophysical research letters **29**:9-1-9-4.

Holz, A., Wood, S.W., Veblen, T.T., Bowman, D.M., 2015. Effects of high-severity fire drove the population collapse of the subalpine Tasmanian endemic conifer Athrotaxis cupressoides. Glob. Change Biol. 21, 445–458.

Hood, S.M., Varner, J.M., van Mantgem, P., Cansler, C.A., 2018. Fire and tree death: understanding and improving modeling of fire-induced tree mortality. Environ. Res. Lett. 13, 113004.

Huang, J., Kautz, M., Trowbridge, A.M., Hammerbacher, A., Raffa, K.F., Adams, H.D., Goodsman, D.W., Xu, C., Meddens, A.J., Kandasamy, D., 2020. Tree defence and bark beetles in a drying world: carbon partitioning, functioning and modelling. New Phytol. 225, 26–36.

Huffman, D.W., Floyd, M.L., Hanna, D.P., Crouse, J.E., Fulé, P.Z., Meador, A.J.S., Springer, J.D., 2020. Fire regimes and structural changes in oak-pine forests of the Mogollon Highlands ecoregion: Implications for ecological restoration. For. Ecol. Manage. 465, 118087.

Hurteau, M.D., Liang, S., Westerling, A.L., Wiedinmyer, C., 2019. Vegetation-fire feedback reduces projected area burned under climate change. Sci. Rep. 9, 1–6.

Iglesias, V., Whitlock, C., 2020. If the trees burn, is the forest lost? Past dynamics in temperate forests help inform management strategies. Philosophical Transactions of the Royal Society B 375, 20190115.

IPCC. 2018. Global Warming of 1.5°C, an IPCC special report on the impacts of global warming of 1.5°C above pre-industrial levels (SR1.5). Intergovernmental Panel on Climate Change (IPCC), Geneva, Switzerland.

Iverson, L.R., McKenzie, D., 2013. Tree-species range shifts in a changing climate: detecting, modeling, assisting. Landscape Ecol. 28, 879–889.

Jackson, J.F., Adams, D.C., Jackson, U.B., 1999. Allometry of constitutive defense: a model and a comparative test with tree bark and fire regime. Am. Nat. 153, 614–632.

Jackson, S.T., Betancourt, J.L., Booth, R.K., Gray, S.T., 2009. Ecology and the ratchet of events: Climate variability, niche dimensions, and species distributions. Proc. Natl. Acad. Sci. 106, 19685–19692.

Jackson, S.T., Blois, J.L., 2015. Community ecology in a changing environment: Perspectives from the Quaternary. Proc. Natl. Acad. Sci. 112, 4915–4921.

Jackson, S.T., Overpeck, J.T., 2000. Responses of plant populations and communities to environmental changes of the late Quaternary. Paleobiology 26, 194–220.

Jackson, S.T., Sax, D.F., 2010. Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. Trends Ecol. Evol. 25, 153–160.

Jain, T.B., Pilliod, D.S., Graham, R.T., Lentile, L.B., Sandquist, J.E., 2012. Index for characterizing post-fire soil environments in temperate coniferous forests. Forests 3, 445–466.

Jentsch, A., White, P., 2019. A theory of pulse dynamics and disturbance in ecology. Ecology e02734.

Jeronimo, S.M.A., Lutz, J.A., Kane, V.R., Larson, A.J., Franklin, J.F., 2020. Burn weather and three-dimensional fuel structure determine post-fire tree mortality. Landscape Ecol.

Johnson, D.M., Domec, J.C., Carter Berry, Z., Schwantes, A.M., McCulloh, K.A., Woodruff, D.R., Wayne Polley, H., Wortemann, R., Swenson, J.J., Scott Mackay, D., 2018. Co-occurring woody species have diverse hydraulic strategies and mortality rates during an extreme drought. Plant, Cell Environ. 41, 576–588.

Johnstone, J.F., Allen, C.D., Franklin, J.F., Frelich, L.E., Harvey, B.J., Higuera, P.E., Mack, M.C., Meentemeyer, R.K., Metz, M.R., Perry, G.L., 2016. Changing disturbance regimes, ecological memory, and forest resilience. Front. Ecol. Environ. 14, 369–378.

Kautz, M., Meddens, A.J., Hall, R.J., Arneth, A., 2017. Biotic disturbances in Northern Hemisphere forests–a synthesis of recent data, uncertainties and implications for forest monitoring and modelling. Glob. Ecol. Biogeogr. 26, 533–552.

Kayes, L.J., Tinker, D.B., 2012. Forest structure and regeneration following a mountain pine beetle epidemic in southeastern Wyoming. For. Ecol. Manage. 263, 57–66.

Keane, R.E., Tomback, D.F., Aubry, C.A., Bower, A.D., Campbell, E.M., Cripps, C.L., Jenkins, M.B., Mahalovich, M.F., Manning, M., McKinney, S.T., Murray, M.P., Perkins, D.L., Reinhart, D.P., Ryan, C., Schoettle, A.W., Smith, C.M., 2012. A range-wide restoration strategy for whitebark pine (<i>Pinus albicaulis</i>). RMRS-GTR-279. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ft. Collins, CO.

Keeley, J.E., 1997. Trace gas emissions and smoke-induced seed germination. Science 276, 1248–1250.

Keeley, J.E., 2009. Ecological foundations for fire management in North American forest and shrubland ecosystems. US Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Keeley, J.E., 2012. Ecology and evolution of pine life histories. Ann. For. Sci. 69, 445–453.

Keeley, J.E., Bond, W.J., Bradstock, R.A., Pausas, J.G., Rundel, P.W., 2011a. Fire in Mediterranean ecosystems: ecology, evolution and management. Cambridge University Press.

Keeley, J.E., Brennan, T.J., 2012. Fire-driven alien invasion in a fire-adapted ecosystem. Oecologia 169, 1043–1052.

Keeley, J.E., Keeley, S.C., 1987. Role of fire in the germination of chaparral herbs and suffrutescents. Madroño:240–249.

Keeley, J.E., Pausas, J.G., 2019. Distinguishing disturbance from perturbations in fire-prone ecosystems. Int. J. Wildland Fire 28, 282–287.

Keeley, J.E., Pausas, J.G., Rundel, P.W., Bond, W.J., Bradstock, R.A., 2011b. Fire as an evolutionary pressure shaping plant traits. Trends Plant Sci. 16, 406–411.

Keeley, J.E., van Mantgem, P., Falk, D.A., 2019. Fire, climate and changing forests. Nat. Plants 5, 774–775.

Keeley, J.E., Zedler, P.H., 1998. Evolution of life histories in pines. In: Richardson, D. (Ed.), Ecology and biogeography of Pinus. Cambridge University Press, Cambridge, UK, pp. 219–249.

Kelly, R., Chipman, M.L., Higuera, P.E., Stefanova, I., Brubaker, L.B., Hu, F.S., 2013. Recent burning of boreal forests exceeds fire regime limits of the past 10,000 years. Proc. Natl. Acad. Sci. 110, 13055–13060.

Kerns, B.K., Tortorelli, C., Day, M.A., Nietupski, T., Barros, A.M., Kim, J.B., Krawchuk, M. A., 2020. Invasive grasses: A new perfect storm for forested ecosystems? For. Ecol. Manage. 463, 117985.

Keyser, A.R., Krofcheck, D.J., Remy, C.C., Allen, C.D., Hurteau, M.D., 2020. Simulated increases in fire activity reinforce shrub conversion in a southwestern US forest. Ecosystems 23, 1702–1713.

Kemp, K.B., Higuera, P.E., Morgan, P., 2016. Fire legacies impact conifer regeneration across environmental gradients in the U.S. northern Rockies. Landscape Ecol. 31, 619–636.

Kidd, K.R., Varner, J.M., 2019. Differential relative bark thickness and aboveground growth discriminates fire resistance among hardwood sprouts in the southern Cascades, California. Trees 33, 267–277.

Kimmerer, R.W., Lake, F.K., 2001. The Role of Indigenous Burning in Land Management. J. Forest. 99, 36–41.

Kitzberger, T., Falk, D.A., Westerling, A.L., Swetnam, T.W., 2017. Direct and indirect climate controls predict heterogeneous early-mid 21st century wildfire burned area across western and boreal North America. PLoS ONE 12, e0188486.

Kitzberger, T., Perry, G., Paritsis, J., Gowda, J., Tepley, A., Holz, A., Veblen, T., 2016. Fire–vegetation feedbacks and alternative states: common mechanisms of temperate forest vulnerability to fire in southern South America and New Zealand. N. Z. J. Botan. 54, 247–272.

Knapp, E.E., Weatherspoon, C.P., Skinner, C.N., 2012. Shrub seed banks in mixed conifer forests of northern California and the role of fire in regulating abundance. Fire Ecol. 8, 32–48.

Krawchuk, M.A., Meigs, G.W., Cartwright, J.M., Coop, J.D., Davis, R., Holz, A., Kolden, C., Meddens, A.J.H., 2020. Disturbance refugia within mosaics of forest fire, drought, and insect outbreaks. Front. Ecol. Environ. 18, 235–244.

Kreye, J.K., Varner, J.M., Hiers, J.K., Mola, J., 2013. Toward a mechanism for eastern North American forest mesophication: differential litter drying across 17 species. Ecol. Appl. 23, 1976–1986.

Lake, F.K., Wright, V., Morgan, P., McFadzen, M., McWethy, D., Stevens-Rumann, C., 2017. Returning Fire to the Land: Celebrating Traditional Knowledge and Fire. J. Forest. 115, 343–353.

Larson, A.J., Franklin, J.F., 2005. Patterns of conifer tree regeneration following an autumn wildfire event in the western Oregon Cascade Range, USA. For. Ecol. Manage. 218, 25–36.

Landesmann, J.B., Tiribelli, F., Paritsis, J., Veblen, T.T., Kitzberger, T., 2021. Increased fire severity triggers positive feedbacks of greater vegetation flammability and favors plant community-type conversions. J. Veg. Sci. 32, e12936.

Laughlin, D.C., Joshi, C., van Bodegom, P.M., Bastow, Z.A., Fulé, P.Z., 2012. A predictive model of community assembly that incorporates intraspecific trait variation. Ecol. Lett. 15, 1291–1299.

Lauvaux, C.A., Skinner, C.N., Taylor, A.H., 2016. High severity fire and mixed conifer forest-chaparral dynamics in the southern Cascade Range, USA. For. Ecol. Manage. 363, 74–85.

Law, D.J., Adams, H.D., Breshears, D.D., Cobb, N.S., Bradford, J.B., Zou, C.B., Field, J.P., Gardea, A.A., Williams, A.P., Huxman, T.E., 2019. Bioclimatic envelopes for individual demographic events driven by extremes: plant mortality from drought and warming. Int. J. Plant Sci. 180, 53–62.

Lawes, M.J., Clarke, P.J., 2011. Ecology of plant resprouting: populations to community responses in fire-prone ecosystems. Plant Ecol. 212, 1937–1943.

Leck, M.A., 2012. Ecology of soil seed banks. Elsevier.

Leslie, A.B., Beaulieu, J.M., Mathews, S., 2017. Variation in seed size is structured by dispersal syndrome and cone morphology in conifers and other nonflowering seed plants. New Phytol. 216, 429–437.

Lindenmayer, D.B., Burton, P.J., Franklin, J.F., 2012. Salvage logging and its ecological consequences. Island Press.

Littlefield, C.E., Dobrowski, S.Z., Abatzoglou, J.T., Parks, S.A., Davis, K.T., 2020. A climatic dipole drives short-and long-term patterns of postfire forest recovery in the western United States. Proc. Natl. Acad. Sci. 117, 29730–29737.

Litzow, M.A., Hunsicker, M.E., 2016. Early warning signals, nonlinearity, and signs of hysteresis in real ecosystems. Ecosphere 7, e01614.

Lloret, F., Batllori, E., 2021. Climate-Induced Global Forest Shifts due to Heatwave-Drought. In: Canadell, J.G., Jackson, R.B. (Eds.), Ecosystem Collapse and Climate Change. Springer International Publishing, Cham, pp. 155–186.

Lloret, F., Escudero, A., Iriondo, J.M., Martínez-Vilalta, J., Valladares, F., 2012. Extreme climatic events and vegetation: the role of stabilizing processes. Glob. Change Biol. 18, 797–805.

Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B., Ackerly, D.D., 2009. The velocity of climate change. Nature 462, 1052–1055.

Luger, A., Moll, E., 1993. Fire protection and afromontane forest expansion in Cape fynbos. Biol. Conserv. 64, 51–56.

Lynch, A.J., Thompson, L.M., Beever, E.A., Cole, D.N., Engman, A.C., Hawkins Hoffman, C., Jackson, S.T., Krabbenhoft, T.J., Lawrence, D.J., Limpinsel, D., Magill, R.T., Melvin, T.A., Morton, J.M., Newman, R.A., Peterson, J.O., Porath, M.T., Rahel, F.J., Schuurman, G.W., Sethi, S.A., Wilkening, J.L., 2021. Managing for RADical ecosystem change: applying the Resist-Accept-Direct (RAD) framework. Frontiers in Ecology and the Environment:fee.2377.

Maherali, H., Pockman, W.T., Jackson, R.B., 2004. Adaptive variation in the vulnerability of woody plants to xylem cavitation. Ecology 85, 2184–2199.

Markesteijn, L., Poorter, L., Bongers, F., Paz, H., Sack, L., 2011. Hydraulics and life history of tropical dry forest tree species: coordination of species' drought and shade tolerance. New Phytol. 191, 480–495.

Marsh, C., Krofcheck, D., Hurteau, M., 2022. Identifying microclimate tree seedling refugia in post-wildfire landscapes. Agric. For. Meteorol. 313, 108741.

Matonis, M.S., Binkley, D., 2018. Not just about the trees: Key role of mosaic-meadows in restoration of ponderosa pine ecosystems. For. Ecol. Manage. 411, 120–131.

Matusick, G., Ruthrof, K.X., Kala, J., Brouwers, N.C., Breshears, D.D., Hardy, G.E.S.J., 2018. Chronic historical drought legacy exacerbates tree mortality and crown dieback during acute heatwave-compounded drought. Environ. Res. Lett. 13, 095002.

McDaniel, J.K., Alexander, H.D., Siegert, C.M., Lashley, M.A., 2021. Shifting tree species composition of upland oak forests alters leaf litter structure, moisture, and flammability. For. Ecol. Manage. 482, 118860.

McDonald, C.J., McPherson, G.R., 2011. Fire behavior characteristics of buffelgrass-fueled fires and native plant community composition in invaded patches. J. Arid Environ. 75, 1147–1154.

McDonald, P.M., Tappeiner, J.C., 1996. Silviculture-ecology of forest-zone hardwoods in the Sierra Nevada. In: Erman, D.C., Erman, D.C. (Eds.). Sierra Nevada Ecosystem Project: Final report to Congress, Vol. III, Assessments and scientific basis for management options, pp. 621–636.

McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? New Phytol. 178, 719–739.

McDowell, N.G., 2011. Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. Plant Physiol. 155, 1051–1059.

McDowell, N.G., Allen, C.D., Anderson-Teixeira, K., Aukema, B.H., Bond-Lamberty, B., Chini, L., Clark, J.S., Dietze, M., Grossiord, C., Hanbury-Brown, A., 2020. Pervasive shifts in forest dynamics in a changing world. Science, 368:eaaz9463.

McDowell, N.G., Sevanto, S., 2010. The mechanisms of carbon starvation: how, when, or does it even occur at all? The New Phytologist 186, 264–266.

McDowell, N.G., Williams, A., Xu, C., Pockman, W., Dickman, L., Sevanto, S., Pangle, R., Limousin, J., Plaut, J., Mackay, D., 2016. Multi-scale predictions of massive conifer mortality due to chronic temperature rise. Nat. Clim. Change 6, 295.

McWethy, D.B., Whitlock, C., Wilmshurst, J.M., McGlone, M.S., Fromont, M., Li, X., Dieffenbacher-Krall, A., Hobbs, W.O., Fritz, S.C., Cook, E.R., 2010. Rapid landscape transformation in South Island, New Zealand, following initial Polynesian settlement. Proc. Natl. Acad. Sci. 107, 21343–21348.

Michalak, J.L., Lawler, J.J., Roberts, D.R., Carroll, C., 2018. Distribution and protection of climatic refugia in North America. Conserv. Biol. 32, 1414–1425.

Michaletz, S.T., Johnson, E.A., 2007. How forest fires kill trees: a review of the fundamental biophysical processes. Scand. J. For. Res. 22, 500–515.

Millar, C.I., Stephenson, N.L., 2015. Temperate forest health in an era of emerging megadisturbance. Science 349, 823–826.

Millar, C.I., Stephenson, N.L., Stephens, S.L., 2007. Climate change and forests of the future: Managing in the face of uncertainty. Ecol. Appl. 17, 2415–12151.

Miller, A.D., Thompson, J.R., Tepley, A.J., Anderson-Teixeira, K.J., 2019. Alternative stable equilibria and critical thresholds created by fire regimes and plant responses in a fire-prone community. Ecography 42, 55–66.

Mittelbach, G.G., Schemske, D.W., 2015. Ecological and evolutionary perspectives on community assembly. Trends Ecol. Evol. 30, 241–247.

McCaughey, W., Schmidt, W., Shearer, R., 1986. Seed-Dispersal Characteristics of Conifers in the Inland Mountain West; General Technical Report INT-203. In: Shearer, R., Shearer, R. (Eds.), Proceedings-Conifer Tree Seed in the Intermountain West Symposium. Ogden, UT, pp. 50–62.

Nagel, T.A., Taylor, A.H., 2005. Fire and persistence of montane chaparral in mixed conifer forest landscapes in the northern Sierra Nevada, Lake Tahoe Basin, California, USA. J. Torrey Bot. Soc. 132, 442–457.

Newberry, B.M., Power, C.R., Abreu, R.C., Durigan, G., Rossatto, D.R., Hoffmann, W.A., 2020. Flammability thresholds or flammability gradients? Determinants of fire across savanna–forest transitions. New Phytol. 228, 910–921.

Niemeyer, R.J., Bladon, K.D., Woodsmith, R.D., 2020. Long-term hydrologic recovery after wildfire and post-fire forest management in the interior Pacific Northwest. Hydrol. Process. 34, 1182–1197.

Nolan, C., Overpeck, J.T., Allen, J.R., Anderson, P.M., Betancourt, J.L., Binney, H.A., Brewer, S., Bush, M.B., Chase, B.M., Cheddadi, R., 2018. Past and future global transformation of terrestrial ecosystems under climate change. Science 361, 920–923.

Nolan, R.H., Collins, L., Leigh, A., Ooi, M.K., Curran, T.J., Fairman, T.A., Resco de Dios, V., Bradstock, R., 2021. Limits to post-fire vegetation recovery under climate change. Plant, Cell Environ. 44, 3471–3489.

North, M.P., Stevens, J.T., Greene, D.F., Coppoletta, M., Knapp, E.E., Latimer, A.M., Restaino, C.M., Tompkins, R.E., Welch, K.R., York, R.A., Young, D.J.N., et al., 2019. Tamm Review: Reforestation for resilience in dry western U.S. forests. For. Ecol. Manage. 432, 209–224.

Notaro, M., Mauss, A., Williams, J.W., 2012. Projected vegetation changes for the American Southwest: combined dynamic modeling and bioclimatic-envelope approach. Ecol. Appl. 22, 1365–1388.

Nowacki, G.J., Abrams, M.D., 2008. The demise of fire and "mesophication" of forests in the eastern United States. Bioscience 58, 123–138.

O'Connor, C.D., Falk, D.A., Lynch, A.M., Swetnam, T.W., Wilcox, C.P., 2017. Disturbance and productivity interactions mediate stability of forest composition and structure. Ecol. Appl. 27, 900–915.

O'Connor, C.D., Falk, D.A., Garfin, G.M., 2020. Projected climate-fire interactions drive forest to shrubland transition on an Arizona Sky Island. Front. Environ. Sci. 8. Article 137. 8:137.

Odion, D.C., Moritz, M.A., DellaSala, D.A., 2010. Alternative community states maintained by fire in the Klamath Mountains, USA. J. Ecol. 98, 96–105.

Ouzts, J., Kolb, T., Huffman, D., Sánchez Meador, A., 2015. Post-fire ponderosa pine regeneration with and without planting in Arizona and New Mexico. For. Ecol. Manage. 354, 281–290.

Owen, S.M., Sieg, C.H., Fulé, P.Z., Gehring, C.A., Baggett, L.S., Iniguez, J.M., Fornwalt, P. J., Battaglia, M.A., 2020. Persistent effects of fire severity on ponderosa pine regeneration niches and seedling growth. For. Ecol. Manage. 477, 118502.

Owen, S.M., Sieg, C.H., Sánchez Meador, A.J., Fulé, P.Z., Iniguez, J.M., Baggett, L.S., Fornwalt, P.J., Battaglia, M.A., 2017. Spatial patterns of ponderosa pine regeneration in high-severity burn patches. For. Ecol. Manage. 405, 134–149.

Parks, S.A., Abatzoglou, J., 2020. Warmer and drier fire seasons contribute to increases in area burned at high severity in western US forests from 1985 to 2017. Geophys. Res. Lett. 47:e2020GL089858.

Parks, S.A., Dobrowski, S.Z., Shaw, J.D., Miller, C., 2019. Living on the edge: trailing edge forests at risk of fire-facilitated conversion to non-forest. Ecosphere 10, e02651.

Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. Syst. 637–669.

Parsons, D.J., DeBenedetti, S.H., 1979. Impact of fire supression on a mixed-conifer forest. For. Ecol. Manage. 2, 21–33.

Pausas, J.G., 2015. Bark thickness and fire regime. Funct. Ecol. 29, 315–327.

Pausas, J.G., Bond, W.J., 2020. Alternative biome states in terrestrial ecosystems. Trends Plant Sci. 25, 250–263.

Pausas, J.G., Keeley, J.E., 2009. A burning story: the role of fire in the history of life. Bioscience 59, 593–601.

Pausas, J.G., Keeley, J.E., 2014. Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. New Phytologist 204, 55–65.

Pausas, J.G., Keeley, J.E., 2017. Epicormic resprouting in fire-prone ecosystems. Trends Plant Sci. 22, 1008–1015.

Pausas, J.G., Keeley, J.E., Schwilk, D.W., 2017. Flammability as an ecological and evolutionary driver. J. Ecol. 105, 289–297.

Pausas, J.G., Paula, S., 2012. Fuel shapes the fire–climate relationship: evidence from Mediterranean ecosystems. Glob. Ecol. Biogeogr. 21, 1074–1082.

Pausas, J.G., Pratt, R.B., Keeley, J.E., Jacobsen, A.L., Ramirez, A.R., Vilagrosa, A., Paula, S., Kaneakua-Pia, I.N., Davis, S.D., 2016. Towards understanding resprouting at the global scale. New Phytol. 209, 945–954.

Peeler, J.L., Smithwick, E.A., 2020. Seed source pattern and terrain have scale-dependent effects on post-fire tree recovery. Landscape Ecol. 35, 1945–1959.

Pellegrini, A.F., Anderegg, W.R., Paine, C.T., Hoffmann, W.A., Kartzinel, T., Rabin, S.S., Sheil, D., Franco, A.C., Pacala, S.W., 2017. Convergence of bark investment according to fire and climate structures ecosystem vulnerability to future change. Ecol. Lett. 20, 307–316.

Pounden, E., Greene, D.F., Michaletz, S.T., 2014. Non-serotinous woody plants behave as aerial seed bank species when a late-summer wildfire coincides with a mast year. Ecol. Evol. 4, 3830–3840.

Prichard, S.J., Hessburg, P.F., Hagmann, R.K., Povak, N.A., Dobrowski, S.Z., Hurteau, M. D., Kane, V.R., Keane, R.E., Kobziar, L.N., Kolden, C.A., 2021. Adapting western North American forests to climate change and wildfires: 10 common questions. Ecol, Appl, p. 31.

Prichard, S.J., Kennedy, M.C., 2012. Fuel treatment effects on tree mortality following wildfire in dry mixed conifer forests, Washington State, USA. Int. J. Wildland Fire 21, 1004–1013.

Ratajczak, Z., Carpenter, S.R., Ives, A.R., Kucharik, C.J., Ramiadantsoa, T., Stegner, M.A., Williams, J.W., Zhang, J., Turner, M.G., 2018. Abrupt change in ecological systems: inference and diagnosis. Trends Ecol. Evol. 33, 513–526.

Ratajczak, Z., Nippert, J.B., Collins, S.L., 2012. Woody encroachment decreases diversity across North American grasslands and savannas. Ecology 93, 697–703.

Redmond, M.D., Weisberg, P.J., Cobb, N.S., Clifford, M.J., 2018. Woodland resilience to regional drought: Dominant controls on tree regeneration following overstorey mortality. J. Ecol. 106, 625–639.

Remke, M.J., Hoang, T., Kolb, T., Gehring, C., Johnson, N.C., Bowker, M.A., 2020. Familiar soil conditions help Pinus ponderosa seedlings cope with warming and drying climate. Restor. Ecol. https://doi.org/10.1111/rec.13144.

Restaino, C., Young, D.J.N., Estes, B., Gross, S., Wuenschel, A., Meyer, M., Safford, H., 2019. Forest structure and climate mediate drought-induced tree mortality in forests of the Sierra Nevada, <span style="font-variant:small-caps;">USA</span>. Ecol. Appl. 29, e01902.

Reynolds, R.T., Meador, A.J.S., Youtz, J.A., Nocolet, T., Matonis, M.S., Jackson, P.L., DeLorenzo, D.G., Graves, A.D., 2013. Restoring composition and structure in Southwestern frequent-fire forests: A science-based framework for improving ecosystem resiliency. Gen. Tech. Rep. RMRS- GTR-310. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Rodman, K.C., Veblen, T.T., Chapman, T.B., Rother, M.T., Wion, A.P., Redmond, M.D., 2020. Limitations to recovery following wildfire in dry forests of southern Colorado and northern New Mexico, USA. Ecol. Appl. 30, e02001.

Roos, C.I., Guiterman, C.H., 2021. Dating the origins of persistent oak shrubfields in northern New Mexico using soil charcoal and dendrochronology. The. Holocene: 09596836211003255.

Roos, C.I., Swetnam, T.W., Ferguson, T., Liebmann, M.J., Loehman, R.A., Welch, J.R., Margolis, E.Q., Guiterman, C.H., Hockaday, W.C., Aiuvalasit, M.J., 2021. Native American fire management at an ancient wildland–urban interface in the Southwest United States. Proc. Natl. Acad. Sci. 118.

Rosell, J.A., 2016. Bark thickness across the angiosperms: more than just fire. New Phytol. 211, 90–102.

Rosell, J.A., Olson, M.E., Anfodillo, T., Martínez-Méndez, N., 2017. Exploring the bark thickness–stem diameter relationship: clues from lianas, successive cambia, monocots and gymnosperms. New Phytol. 215, 569–581.

Rother, M.T., Veblen, T.T., 2016. Limited conifer regeneration following wildfires in dry ponderosa pine forests of the Colorado Front Range. Ecosphere 7, e01594.

Rother, M.T., Veblen, T.T., Furman, L.G., 2015. A field experiment informs expected patterns of conifer regeneration after disturbance under changing climate conditions. Can. J. For. Res. 45, 1607–1616.

Rowe, J.S., 1983. Concepts of fire effects on plant individuals and species. In: Wein, R. W., Maclean, D.A. (Eds.), The role of fire in northern circumpolar ecosystems. John Wiley & Sons, New York, pp. 135–154.

Ruthrof, K.X., Breshears, D.D., Fontaine, J.B., Froend, R.H., Matusick, G., Kala, J., Miller, B.P., Mitchell, P.J., Wilson, S.K., van Keulen, M., 2018. Subcontinental heat wave triggers terrestrial and marine, multi-taxa responses. Sci. Rep. 8, 13094.

Ryan, K.C., Reinhardt, E.D., 1988. Predicting postfire mortality of seven western conifers. Can. J. For. Res. 18, 1291–1297.

Saatkamp, A., Poschlod, P., Venable, D.L., 2014. The Functional Role of Soil Seed Banks in Natural Communities. In: Gallagher, R.S. (Ed.), The ecology of regeneration in plant communities. CAB International, Wallingford, UK, pp. 263–295.

Sade, N., Gebremedhin, A., Moshelion, M., 2012. Risk-taking plants: anisohydric behavior as a stress-resistance trait. Plant Signaling Behav. 7, 767–770.

Safford, H.D., Van de Water, K.M., 2014. Using fire return interval departure (FRID) analysis to map spatial and temporal changes in fire frequency on national forest lands in California. Res. Pap. PSW-RP-266. Albany, CA: US Department of Agriculture, Forest Service, Pacific Southwest Research Station, 59, p **266**.

Safford, H.D., Stevens, J.T., 2017. Natural range of variation for yellow pine and mixed-conifer forests in the Sierra Nevada, southern Cascades, and Modoc and Inyo National Forests, California, USA. Gen. Tech. Rep. PSW-GTR-256. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, 229, p. 256.

Sala, A., Piper, F., Hoch, G., 2010. Physiological mechanisms of drought-induced tree mortality are far from being resolved. New Phytol. 186, 274–281.

Sankaran, M., 2019. Droughts and the ecological future of tropical savanna vegetation. J. Ecol. 107, 1531–1549.

Sapes, G., Demaree, P., Lekberg, Y., Sala, A., 2021. Plant carbohydrate depletion impairs water relations and spreads via ectomycorrhizal networks. New Phytol. 229, 3172–3183.

Savage, M., Mast, J.N., 2005. How resilient are southwestern ponderosa pine forests after crown fires? Can. J. For. Res. 35, 967–977.

Savage, M., Mast, J.N., Feddema, J.J., 2013. Double whammy: high-severity fire and drought in ponderosa pine forests of the Southwest. Can. J. For. Res. 43, 570–583.

Scheffers, B.R., De Meester, L., Bridge, T.C.L., Hoffmann, A.A., Pandolfi, J.M., Corlett, R. T., Butchart, S.H.M., Pearce-Kelly, P., Kovacs, K.M., Dudgeon, D., 2016. The broad footprint of climate change from genes to biomes to people. Science 354 (aaf7671).

Schubert, A., Nano, C., Clarke, P.J., Lawes, M., 2016. Evidence for bark thickness as a fire-resistance trait from desert to savanna in fire-prone inland Australia. Plant Ecol. 217, 683–696.

Schuurman, G.W., Hawkins-Hoffman, C., Cole, D.N., Lawrence, D.J., Morton, J.M., Magness, D.R., Cravens, A.E., Covington, S., O'Malley, R., Fisichelli, N.A., 2020. Resist-Accept-Direct (RAD)—A Framework for the 21st-century Natural Resource Manager. Natural Resource Report NPS/NRSS/CCRP/NRR—2020/ 2213. National Park Service, Fort Collins, Colorado.

Schwilk, D.W., Ackerly, D.D., 2001. Flammability and serotiny as strategies: correlated evolution in pines. Oikos 94, 326–336.

Schwilk, D.W., Gaetani, M.S., Poulos, H.M., 2013. Oak bark allometry and fire survival strategies in the Chihuahuan Desert Sky Islands, Texas, USA. PLoS ONE 8, e79285.

Schwilk, D.W., Keeley, J.E., 2006. The role of fire refugia in the distribution of Pinus sabiniana (Pinaceae) in the southern Sierra Nevada. Madrono 53, 364–372.

Senf, C., Buras, A., Zang, C.S., Rammig, A., Seidl, R., 2020. Excess forest mortality is consistently linked to drought across Europe. Nat. Commun. 11, 1–8.

Shirk, A.J., Cushman, S.A., Waring, K.M., Wehenkel, C.A., Leal-Sáenz, A., Toney, C., Lopez-Sanchez, C.A., 2018. Southwestern white pine (Pinus strobiformis) species distribution models project a large range shift and contraction due to regional climatic changes. For. Ecol. Manage. 411, 176–186.

Shive, K.L., Preisler, H.K., Welch, K.R., Safford, H.D., Butz, R.J., O'Hara, K.L., Stephens, S.L., 2018. From the stand scale to the landscape scale: predicting the spatial patterns of forest regeneration after disturbance. Ecological. Applications.

Sidman, G., Guertin, D.P., Goodrich, D.C., Thoma, D., Falk, D., Burns, I.S., 2016. A coupled modelling approach to assess the effect of fuel treatments on post-wildfire runoff and erosion. Int. J. Wildland Fire 25, 351–362.

Simeone, C., Maneta, M.P., Holden, Z.A., Sapes, G., Sala, A., Dobrowski, S.Z., 2019. Coupled ecohydrology and plant hydraulics modeling predicts ponderosa pine seedling mortality and lower treeline in the US Northern Rocky Mountains. New Phytol. 221, 1814–1830.

Singleton, M.P., Thode, A.E., Meador, A.J.S., Iniguez, J.M., 2019. Increasing trends in high-severity fire in the southwestern USA from 1984 to 2015. For. Ecol. Manage. 433, 709–719.

Smit, I.P., Asner, G.P., Govender, N., Kennedy-Bowdoin, T., Knapp, D.E., Jacobson, J., 2010. Effects of fire on woody vegetation structure in African savanna. Ecol. Appl. 20, 1865–1875.

Smith, A.E., Smith, F.W., 2005. Twenty-year change in aspen dominance in pure aspen and mixed aspen/conifer stands on the Uncompahgre Plateau, Colorado, USA. For. Ecol. Manage. 213, 338–348.

Smith, K.T., Arbellay, E., Falk, D.A., Sutherland, E.K., 2016. Macroanatomy and compartmentalization of recent fire scars in three North American conifers. Can. J. For. Res. 46, 535–542.

Staver, A.C., Archibald, S., Levin, S.A., 2011. The Global Extent and Determinants of Savanna and Forest as Alternative Biome States. Science 334, 230–232.

Steel, Z.L., Foster, D., Coppoletta, M., Lydersen, J.M., Stephens, S.L., Paudel, A., Markwith, S.H., Merriam, K., Collins, B.M., 2021. Ecological resilience and vegetation transition in the face of two successive large wildfires. J. Ecol.

Steel, Z.L., Koontz, M.J., Safford, H.D., 2018. The changing landscape of wildfire: burn pattern trends and implications for California's yellow pine and mixed conifer forests. Landscape Ecol. 33, 1–18.

Stephens, S.L., Collins, B.M., Fettig, C.J., Finney, M.A., Hoffman, C.M., Knapp, E.E., North, M.P., Safford, H., Wayman, R.B., 2018. Drought, tree mortality, and wildfire in forests adapted to frequent fire. Bioscience 68, 77–88.

Stephens, S.L., Moghaddas, J.J., 2005. Experimental fuel treatment impacts on forest structure, potential fire behavior, and predicted tree mortality in a California mixed conifer forest. For. Ecol. Manage. 215, 21–36.

Stevens-Rumann, C.S., Kemp, K.B., Higuera, P.E., Harvey, B.J., Rother, M.T., Donato, D. C., Morgan, P., Veblen, T.T., 2018. Evidence for declining forest resilience to wildfires under climate change. Ecol. Lett. 21, 243–252.

Stevens-Rumann, C.S., Morgan, P., 2019. Tree regeneration following wildfires in the western US: a review. Fire Ecol. 15, 1–17.

Stevens, J., Falk, D.A., 2009. Can buffelgrass invasions be controlled in the American Southwest? Using invasion ecology theory to understand buffelgrass success and develop comprehensive restoration and management. Ecological Restoration 27, 417–427.

Stevens, J.T., Collins, B.M., Miller, J.D., North, M.P., Stephens, S.L., 2017a. Changing spatial patterns of stand-replacing fire in California conifer forests. For. Ecol. Manage. 406, 28–36.

Stevens, J.T., Haffey, C.M., Coop, J.D., Fornwalt, P.J., Yocom, L., Allen, C.D., Bradley, A., Burney, O.T., Carril, D., Chambers, M.E., et al., 2021. Tamm Review: Postfire landscape management in frequent-fire conifer forests of the southwestern United States. For. Ecol. Manage. 502, 119678.

Stevens, N., Lehmann, C.E., Murphy, B.P., Durigan, G., 2017b. Savanna woody encroachment is widespread across three continents. Glob. Change Biol. 23, 235–244.

Stewart, J.A., van Mantgem, P.J., Young, D.J., Shive, K.L., Preisler, H.K., Das, A.J., Stephenson, N.L., Keeley, J.E., Safford, H.D., Wright, M.C., 2021. Effects of postfire climate and seed availability on postfire conifer regeneration. Ecol. Appl. 31, e02280.

Stoddard, M.T., Roccaforte, J.P., Meador, A.J.S., Huffman, D.W., Fulé, P.Z., Waltz, A.E. M., Covington, W.W., 2021. Ecological restoration guided by historical reference conditions can increase resilience to climate change of southwestern U.S. Ponderosa pine forests. Forest Ecology and Management **493**:119256.

Suding, K.N., Hobbs, R.J., 2009. Threshold models in restoration and conservation: a developing framework. Trends Ecol. Evol. 24, 271–279.

Syphard, A.D., Brennan, T.J., Keeley, J.E., 2018. Chaparral landscape conversion in southern California. Valuing Chaparral. Springer, pp. 323–346.

Syphard, A.D., Brennan, T.J., Keeley, J.E., 2019. Drivers of chaparral type conversion to herbaceous vegetation in coastal Southern California. Divers. Distrib. 25, 90–101.

Talluto, M.V., Boulangeat, I., Vissault, S., Thuiller, W., Gravel, D., 2017. Extinction debt and colonization credit delay range shifts of eastern North American trees. Nat. Ecol. Evol. 1, 0182.

Tautenhahn, S., Lichstein, J.W., Jung, M., Kattge, J., Bohlman, S.A., Heilmeier, H., Prokushkin, A., Kahl, A., Wirth, C., 2016. Dispersal limitation drives successional pathways in Central Siberian forests under current and intensified fire regimes. Glob. Change Biol. 22, 2178–2197.

Temperton, V.M., Hobbs, R.J., Nuttle, T., Halle, S. (Eds.), 2004. Assembly rules and restoration ecology. Island Press, Washington, DC.

Tepley, A.J., Hood, S.M., Keyes, C.R., Sala, A., 2020. Forest restoration treatments in a ponderosa pine forest enhance physiological activity and growth under climatic stress. Ecol. Appl. 30, e02188.

Tepley, A.J., Thomann, E., Veblen, T.T., Perry, G.L., Holz, A., Paritsis, J., Kitzberger, T., Anderson-Teixeira, K.J., 2018. Influences of fire–vegetation feedbacks and post-fire recovery rates on forest landscape vulnerability to altered fire regimes. J. Ecol. 106, 1925–1940.

Tepley, A.J., Thompson, J.R., Epstein, H.E., Anderson-Teixeira, K.J., 2017. Vulnerability to forest loss through altered postfire recovery dynamics in a warming climate in the Klamath Mountains. Glob. Change Biol. 23, 4117–4132.

Tercero-Bucardo, N., Kitzberger, T., Veblen, T.T., Raffaele, E., 2007. A field experiment on climatic and herbivore impacts on post-fire tree regeneration in north-western Patagonia. J. Ecol. 95, 771–779.

Thomas, C.D., 2010. Climate, climate change and range boundaries. Divers. Distrib. 16, 488–495.

Trenberth, K.E., Dai, A., Van Der Schrier, G., Jones, P.D., Barichivich, J., Briffa, K.R., Sheffield, J., 2014. Global warming and changes in drought. Nat. Clim. Change 4, 17–22.

Trugman, A.T., Anderegg, L.D., Shaw, J.D., Anderegg, W.R., 2020. Trait velocities reveal that mortality has driven widespread coordinated shifts in forest hydraulic trait composition. Proc. Natl. Acad. Sci. 117, 8532–8538.

Tubbesing, C.L., Young, D.J., York, R.A., Stephens, S.L., Battles, J.J., 2021. Incorporating Shrub Neighborhood Dynamics to Predict Forest Succession Trajectories in an Altered Fire Regime. Ecosystems:1–19.

Turner, M.G., Romme, W.H., Gardner, R.H., Hargrove, W.W., 1997. Effects of fire size and pattern on early succession in yellowstone national park. Ecol. Monogr. 67, 411–433.

Turner, M.G., Baker, W.L., Peterson, C.J., Peet, R.K., 1998. Factors Influencing Succession: Lessons from Large, Infrequent Natural Disturbances. Ecosystems 1, 511–523.

Turner, M.G., Braziunas, K.H., Hansen, W.D., Harvey, B.J., 2019. Short-interval severe fire erodes the resilience of subalpine lodgepole pine forests. Proc. Natl. Acad. Sci. 116, 11319–11328.

Turner, M.G., Calder, W.J., Cumming, G.S., Hughes, T.P., Jentsch, A., LaDeau, S.L., Lenton, T.M., Shuman, B.N., Turetsky, M.R., Ratajczak, Z., 2020. Climate change, ecosystems and abrupt change: science priorities. Philosophical Transactions of the Royal Society B 375, 20190105.

Urza, A.K., Sibold, J.S., 2017. Climate and seed availability initiate alternate post-fire trajectories in a lower subalpine forest. J. Veg. Sci. 28, 43–56.

USDA-US Forest Service, 2021. Fire Effects Information System. Rocky Mountain Research Station, Ft. Collins CO. https://www.feis-crs.org/feis/.

Van de Water, K.M., Safford, H.D., 2011. A summary of fire frequency estimates for California vegetation before Euro-American settlement. Fire Ecol. 7, 26–58.

van Mantgem, E.F., van Mantgem, P.J., Falk, D., Keeley, J., 2020a. Linking diverse terminology to vegetation type-conversion, a complex emergent property: Research Synthesis for Resource Managers. California Fire Science Consortium.

van Mantgem, P.J., Caprio, A.C., Stephenson, N.L., Das, A.J., 2016. Does prescribed fire promote resistance to drought in low elevation forests of the Sierra Nevada, California, USA? Fire Ecol. 12, 13–25.

van Mantgem, P.J., Falk, D.A., Williams, E.C., Das, A.J., Stephenson, N.L., 2018. Pre-fire drought and competition mediate post-fire conifer mortality in western U.S. National Parks. Ecol. Appl. 28, 1730–1739.

van Mantgem, P.J., Falk, D.A., Williams, E.C., Das, A.J., Stephenson, N.L., 2020b. The influence of pre-fire growth patterns on post-fire tree mortality for common conifers in western US parks. Int. J. Wildland Fire 29, 513–518.

van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fule, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., 2009. Widespread increase of tree mortality rates in the western United States. Science 323, 521–524.

Vander Wall, S.B., 1992. The role of animals in dispersing a 'wind-dispersed' pine. Ecology 73, 614–621.

Vander Wall, S.B., 2008. On the relative contributions of wind vs. animals to seed dispersal of four Sierra Nevada pines. Ecology 89, 1837–1849.

Varner, J.M., Kane, J.M., Hiers, J.K., Kreye, J.K., Veldman, J.W., 2016. Suites of fire-adapted traits of oaks in the southeastern USA: multiple strategies for persistence. Fire Ecol. 12, 48–64.

Vilagrosa, A., Chirino, E., Peguero-Pina, J.-J., Barigah, T.S., Cochard, H., Gil-Pelegrin, E., 2012. Xylem cavitation and embolism in plants living in water-limited ecosystems. In: Plant responses to drought stress. Springer, pp. 63–109.

Walker, R.B., Coop, J.D., Parks, S.A., Trader, L., 2018. Fire regimes approaching historic norms reduce wildfire-facilitated conversion from forest to non-forest. Ecosphere 9.

Webb, T.I., 1986. Is vegetation in equilibrium with climate? How to interpret late-Quaternary pollen data. Vegetatio 67, 75–91.

Webster, K.M., Halpern, C.B., 2010. Long-term vegetation responses to reintroduction and repeated use of fire in mixed-conifer forests of the Sierra Nevada. Ecosphere 1, 1–27.

Weed, A.S., Ayres, M.P., Hicke, J.A., 2013. Consequences of climate change for biotic disturbances in North American forests. Ecol. Monogr. 83, 441–470.

Wei, R., Yang, G., Zhang, J., Wang, X., Zhou, X., 2020. The thermal insulation properties of oak (Quercus mongolica) bark and the applicability of stem heating models. Int. J. Wildland Fire 28, 969–980.

Welch, K.R., Safford, H.D., Young, T.P., 2016. Predicting conifer establishment post wildfire in mixed conifer forests of the North American Mediterranean-climate zone. Ecosphere 7, e01609.

Wells, P.V., 1969. The relation between mode of reproduction and extent of speciation in woody genera of the California chaparral. Evolution 23, 264–267.

Werner, C.M., Young, D.J., Safford, H.D., Young, T.P., 2019. Decreased snowpack and warmer temperatures reduce the negative effects of interspecific competitors on regenerating conifers. Oecologia 191, 731–743.

Westerling, A.L., 2016. Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. Philosophical Transactions of the Royal Society B: Biological Sciences 371, 20150178.

Westman, W.E., 1978. Measuring the inertia and resilience of ecosystems. Bioscience 28, 705–710.

Whitman, E., Parisien, M.-A., Thompson, D.K., Flannigan, M.D., 2019. Short-interval wildfire and drought overwhelm boreal forest resilience. Sci. Rep. 9, 1–12.

Whittaker, R.H., 1960. Vegetation of the Siskiyou mountains, Oregon and California. Ecol. Monogr. 30, 279–338.

Williams, A.P., Abatzoglou, J.T., Gershunov, A., Guzman-Morales, J., Bishop, D.A., Balch, J.K., Lettenmaier, D.P., 2019. Observed impacts of anthropogenic climate change on wildfire in California. Earth's Future 7, 892–910.

Williams, J.W., Jackson, S.T., Kutzbach, J.E., 2007. Projected distributions of novel and disappearing climates by 2100 AD. Proc. Natl. Acad. Sci. 104, 5738–5742.

Williams, R., Cook, G., Gill, A., Moore, P., 1999. Fire regime, fire intensity and tree survival in a tropical savanna in northern Australia. Aust. J. Ecol. 24, 50–59.

Williams, T.J., Tomback, D.F., Grevstad, N., Broms, K., 2020. Temporal and energetic drivers of seed resource use by Clark's nutcracker, keystone seed disperser of coniferous forests. Ecosphere 11, e03085.

Wolf, K.D., Higuera, P.E., Davis, K.T., Dobrowski, S.Z., 2021. Wildfire impacts on forest microclimate vary with biophysical context. Ecosphere 12, e03467.

Wright, M.C., van Mantgem, P., Stephenson, N.L., Das, A.J., Keeley, J.E., 2021. Seed production patterns of surviving Sierra Nevada conifers show minimal change following drought. For. Ecol. Manage. 480, 118598.

Young, D., Meyer, M., Estes, B., Gross, S., Wuenschel, A., Restaino, C., Safford, H., 2020a. Forest recovery following extreme drought in California, USA: natural patterns and effects of pre-drought management. Ecol. Appl. 1, e2002.

Young, D.J., Blush, T.D., Landram, M., Wright, J.W., Latimer, A.M., Safford, H.D., 2020b. Assisted gene flow in the context of large-scale forest management in California, USA. Ecosphere 11, e03001.

Young, D.J., Werner, C.M., Welch, K.R., Young, T.P., Safford, H.D., Latimer, A.M., 2019. Post-fire forest regeneration shows limited climate tracking and potential for drought-induced type conversion. Ecology 100, e02571.

Zargar, A., Sadiq, R., Naser, B., Khan, F.I., 2011. A review of drought indices. Environmental Reviews 19, 333–349.

Zedler, P.H., 1995. Are some plants born to burn? Trends Ecol. Evol. 10, 393–395.

Zeppel, M.J.B., Harrison, S.P., Adams, H.D., Kelley, D.I., Li, G., Tissue, D.T., Dawson, T. E., Fensham, R., Medlyn, B.E., Palmer, A., West, A.G., McDowell, N.G., 2015. Drought and resprouting plants. New Phytol. 206, 583–589.